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# Studies on the Charopidae of tropical and subtropical Australia. I. *Oreokera*: A primitive genus from the high mountains of North Queensland (Mollusca : Pulmonata : Charopidae)

by John Stanisic

Queensland Museum, Brisbane

## ABSTRACT

The charopid genus *Oreokera* is shown to be an invalidly introduced taxon. It is herein formally validated and redefined. The genus contains two species found only on the summits of the high mountains of north-east Queensland. The type species, *Oreokera cumulus* (Odhner, 1917) is redescribed and refigured on the basis of newly dissected topotypic material. A new species, *Oreokera nimbus* from Thornton Peak, is figured and described. *Oreokera* is identified as a primitive taxon among the Charopidae by the absence of a closed secondary ureter in either *O. cumulus* or *O. nimbus*. The relationships of the genus are discussed and some comments made on its biogeographic status.

## INTRODUCTION

The Australian Charopidae has traditionally been viewed as a group which shows its greatest diversity in the cool temperate forests of south-east Australia. However, recent collecting in Queensland and northern New South Wales has revealed a remarkable radiation in the sub-tropical and tropical rainforests. Particularly significant is the charopid diversity shown by the group on the high mountains of north east Queensland. The Charopidae, as a widespread and ancient group, has the potential to provide significant data on the biogeography of this area, but a primary barrier to the initiation of these studies has been lack of material. Until recently, knowledge of the molluscan fauna on these peaks rested with a species list (10) prepared by Charles Hedley (1889) after an early expedition up Mt Bellenden Ker (Meston, 1889) and several sporadic collections including the 1910-1913 Swedish Scientific Expedition.

In 1981 an expedition by Queensland Museum staff and volunteers, sponsored by the American-based Earthwatch organisation, collected 46 species of terrestrial mollusc from Mt Bellenden Ker. Of these, 22 species were collected from the summit, including 10 species not found at altitudes lower than 1000m. These results indicated a strong altitudinal stratification among the land snails similar to that shown by the plants and insects. Most notable from a biogeographical viewpoint



however, was the large number of charopids — 10 species, of which 6 did not occur under 1000m (Stanisic, unpublished). Only one, *Oreokera cumulus* (Odhner, 1917), had been previously described.

## SYSTEMATIC REVIEW

The following treatment of *Oreokera* is based on the limited amount of material in the Queensland Museum (QMMO) and Australian Museum, Sydney (AMC). Although Nils Odhner described '*Flammulina' cumulus* in 1917, further additions to the material available for study have been made only recently and largely through the efforts of entomologist Dr Geoff Monteith. While this has enabled an adequate description of *Oreokera cumulus* (Odhner, 1917) and *O. nimbus*, material is still limited.

*Oreokera*, has a disjunct distribution on the mountains and plateaux above 1000 metres in the tropical rainforest region of north-east Queensland (Fig. 1). *O. cumulus* is the more widespread, occurring on several peaks from Mt Bartle-Frere in the south to Devil's Thumb, south-east of Mossman in the north. *O. nimbus* has been found only on Thornton Peak, north of the Daintree River. Both species are confined to altitudes above 1000m where rainfall is high and the forest types are environmentally similar to the temperate forests of southern Australia.

## GENUS *OREOKERA* NEW GENUS

*Oreokera* Iredale, 1933, Records Australian Mus., 19(1): 54; Iredale, 1937, Australian Zool, 8(4): 318; Iredale, 1941, Australian Nat., 10(8): 264 — nude names.

### Diagnosis

Shell medium to large, spire moderately to strongly elevated. Apical whorls with prominent spiral cords, fewer and more regular in *cumulus* (Plate 1a-b) than *nimbus* (Plate 2a-b), with a secondary sculpture of vague radial rugosities on the last portion (Plate 1a). Post apical sculpture complex, of regularly spaced, very prominent radial ribs with well developed periostracal blades (Plate 2c). Microsculpture of prominent radial riblets crossed by finer microspiral cordlets, more numerous in *cumulus* than *nimbus* (Plates 1c-d, 2d-e). Sculpture not reduced below periphery and continuous on base (Plate 2f). Periphery acutely rounded to keeled (Plate 2b,e). Body whorl not descending. Lip simple with well developed parietal callus. Shell colour yellow-horn to brown with darker flammulations above and below (Figs 2a,c,d,f). Genitalia with bilobed ovotestis oriented at right angles to plan of coiling, strongly kinked hermaphroditic duct, talon and carrefour without unusual features (Figs 3d, 4b, 4d, 5b, 5c, 5e). Albumen gland, prostate and uterus typical (Fig. 3b,d). Penis moderately (*cumulus*) to strongly (*nimbus*) swollen (Figs 3c, 5a), internally with complex (*nimbus*) to simple (*cumulus*) pilasters (figs 4a, 5d). Epiphallus well developed, reflexed, with accessory caecum and moderately long (*nimbus*) to very long (*cumulus*) flagellum entering penis through a verge (*nimbus*) or simple pore (*cumulus*) (Figs 3c, 5a). Penial retractor muscle short, inserting on the epiphallic caecum (Fig. 5d). Vas deferens a simple tube (Figs 3c, 5b). Spermatheca typical. Free oviduct short, almost as long as vagina. Vagina and atrium short (Figs 3a, 5a), internally with longitudinal pilasters. Pallial cavity with no secondary ureter, kidney with much reduced rectal lobe and prominent pericardial lobe (Figs 4c, 5f). Pallial roof pigmented, with slight intrusion of mantle gland. Animal darkly pigmented above. Radula with tricuspid central tooth that has the mesocone almost twice the length of the endocone and ectocone. Inner laterals similar, lateromarginals with mesocone reduced and endocone split. Marginals with complex endo- and ectoconal cusps, mesocone reduced (Plate 2e-f).

**Type Species:** *Flammulina cumulus* Odhner, 1917

### Comparisons

The extremely prominent radial ribs, keel, elevated spire, almost closed umbilicus, apical spiral cords and strongly reticulate postnuclear microsculpture of *Oreokera* are a combination of shell characters not found in any other north-east Queensland charopid. *Mussonula* Iredale, 1937 from south-east Queensland, has a narrowed umbilicus, strongly radial sculpture on the post apical



whorls, elevated spire and spirally striate protoconch, but lacks the flammulations and post nucleur microsculpture of *Oreokera* and is less than half the size. *Hedleyoconcha* Pilsbry, 1893 from northern New South Wales and southern Queensland has an elevated spire and almost closed umbilicus but differs in having reduced post apical sculpture of low radials and low broad spirals as well as a pustulose protoconch.

The main features characterising *Oreokera* are in its anatomy. The absence of a secondary ureter, kinked hermaphroditic duct, orientation of the ovotestis and accessory appendages on the male genitalia are basic departures from the charopid patterns discussed by Solem (1983). While some of these may be secondary modifications associated with the arboreal lifestyle and altered shell shape of *Oreokera*, the absence of a secondary ureter identifies it as a primitive taxon among the Charopidae. The posteriorly opening ureter (Figs 4c, 5f) is typical among the Pacific Island Endodontidae. Solem (1976, pp. 84-87) discussed the significance of the closed ureter in the Charopidae and considered this a major advance over the incomplete or absent secondary ureter.

### Key to the Species of *Oreokera*

1. Spiral cords on protoconch mainly regular, diameter of protoconch 885µm at 1½ whorls; adult microsculpture with microspirals less widely spaced than radial riblets; penis interior with main pilaster, no verge; epiphallic flagellum long, 4 times length of penis (Figs 2a-c, 3a-d, 4a-d, Plate 1a-f).....*Oreokera cumulus* (Odhner, 1917)
2. Spiral cords on protoconch mainly squiggly, diameter of protoconch 1065µm at 1½ whorls; adult microsculpture with microspirals equally or more widely spaced than radial riblets; penis interior with complex pilasters, verge present; epiphallic caecum short, 2 times length of penis (Figs 2d-f, 5a-f, Plate 2a-f).....*Oreokera nimbus* sp. nov.

### Nomenclature and Previous Studies

Iredale (1933) introduced the taxon *Oreokera* as follows: "As the species (referring to *F. cumulus*) is certainly not conchologically referable to the genus *Flammulina*, the new genus *Oreokera* is proposed for it." Solem (1964, p. 46; 1979, pp. 46, 92) and Smith and Kershaw (1985, pp. 1-2) have justifiably argued that a number of taxa introduced in that publication (Iredale, 1933) were *nomina nuda* because of little or no accompanying description. For similar reasons Iredale's introduction of *Oreokera* is considered invalid. In some instances Iredale subsequently validated these poorly proposed taxa. However, this was not the case with *Oreokera* which only appeared as an entry in his later check list (Iredale, 1937 p. 318). In order to maintain consistency with the views of the above authors, the name *Oreokera* is retained but herein validated.

Odhner (1917) assigned *O. cumulus* to the New Zealand genus *Flammulina* Martens, 1873 and near to *Helix corticicola* Cox, 1866 from southern Queensland on the basis of overall conchological similarity. Iredale (1933) on the basis of the reasons given above, rejected Odhner's association, considered that these two species deserved separate generic recognition and invalidly introduced the taxon *Oreokera* to accommodate them. Rather fortuitously the present study shows Iredale to be partly correct in that *Flammulina* shows major differences in pallial and genital anatomy which suggest that any conchological consistencies with *Oreokera* are convergent (See Solem, 1983, p. 64, fig. 29).

It is highly doubtful if Iredale ever viewed the type or any other specimen of *O. cumulus*. It is, however, more probable that his association of *H. corticicola* with the Bellenden Ker species was based solely on Odhner's earlier assessment. Besides anatomical differences (Stanisic, unpublished) there are major conchological differences between these two species. *H. corticicola* has a radially sculptured protoconch, less intricate microsculpture and quite different coiling pattern to *O. cumulus*. *Oreokera dorrigensis* Iredale, 1941 was included here by Iredale on the basis of its similarity to *H. corticicola*. While these two latter species show acceptable generic level similarity to each other, they are excluded from *Oreokera* as herein defined and will be discussed elsewhere.

### Distribution and Basic Ecology

*Oreokera* ranges from Mt Bartle-Frere at the southern end of the Bellenden Ker Range to Thornton Peak in the north. In between it occurs at Mt Bellenden Ker, Devil's Thumb (near Mossman), Mt Lewis and Black Mountain (near Julatten). There are no records from the Atherton Tableland, Graham Range, Windsor Tableland or the more northerly peaks of the Daintree to Bloomfield rainforest. It is restricted to the simple microphyll vine fern forests and thickets occurring on these peaks, at altitudes near or above 1000m.

Collecting efforts in the Atherton Tableland and Graham Range have been sufficient to indicate that its absence from these areas is real. There is still hope of finding *Oreokera* at localities such as Mt Spurgeon (alt. 1341m) and Mt Finnegan (alt. 1148m). The disjunct, restricted distribution of *Oreokera* is at first glance remarkable, but has a number of counterparts in plant and other invertebrate groups and its significance will be discussed further below.

*Oreokera* has been collected in arboreal ('axils of palm fronds') and semi-arboreal ('under bark of rotting logs') situations. It has not yet been found live in the litter.

### **OREOKERA CUMULUS (ODHNER, 1917)** (Plate 1a-f; Figs 2a-c, 3a-d, 4a-d)

*Flammulina cumulus* Odhner, 1917, Kungl. svensk. Vetens. Handl., 52(16): 84, pl. 3. figs 89-91 — Mt Bellenden Ker, NE Queensland, 4000ft.

*Oreokera cumulus* (Odhner), Iredale, 1933, Records Australian Mus., 19: 54; Iredale, 1937, Australian Zool., 8(4): 318.

### Comparative Remarks

*Oreokera cumulus* (Odhner, 1917) is recognisable by its almost closed umbilicus, flammulated shell with strong radial sculpture (figs a-c), relatively large size (mean diameter 6.64mm), elevated spire (mean H/D ratio 0.67) with spirally striate protoconch (Plate 1a), and its range south of the Daintree River (Fig. 1).

*Oreokera cumulus* is larger and has a greater mean whorl count than *O. nimbus* but differs most obviously in having fewer and more regular apical cords and more crowded microspirals on the postnuclear whorls (Plate 1a, 1c). Genital differences include a longer epiphallal flagellum, simple penial pilaster pattern and the absence of a verge in *O. cumulus* (Figs 3c, 4a). These features contrast with the shortened flagellum, more complex penial pilasters and prominent penial verge found in *O. nimbus* (Figs 5a, 5d),

TABLE 1: Local variation in *Oreokera cumulus* (Odhner, 1917)

LOCALITY	NUMBER OF ADULTS MEASURED	RIBS ON BODY WHORL	RIBS PER MM	HEIGHT (MM)	DIAMETER (MM)	H/D	WHORLS
Mt Bellenden Ker QMMO. 14765	1	49	2.21	5.19	7.06	0.74	5¼
Devil's Thumb QMMO. 15444	1	76	4.31	3.57	5.62	0.64	4¾
Black Mtn. QMMO. 15430 AMC.149591	5	74.2 (70- 83)	3.50 (3.12- 3.93)	4.48 (4.34- 4.60)	6.76 (6.30- 7.15)	0.66 (0.62- 0.69)	4⅞+ (4¾- 5)

### Holotype

Naturhistoriska Riksmuseet, Stockholm, E. Mjoberg, May, 1913. (1 live specimen).



## Material Studied

### North East Queensland:

Mt Bellenden Ker, summit, 1560m, SMVFT (1 specimen, QMMO.11274, 1-7 Nov. 1981, Earthwatch/QM); Mt Lewis Road, via Julatten (1 specimen, QMMO.16126, 12 Oct. 1980, G.B. Monteith); Mt Lewis, ca 17.8km along Julatten — Mt Lewis Road, litter, MVFF (1 specimen QMMO.14760, 27 Jun. 1983, J. Stanisic, D. Potter); Leichhardt Ck crossing on Mt Lewis Road, Mt Lewis, litter, SMVFF (1 specimen, QMMO.14756, 1 Oct 1980, J. Stanisic); Black Mountain, 17km ESE of Julatten, 800-1000m (6 specimens, AMC.149591, QMMO.15430 29-30 Apr. 1982, G.B. Monteith, D. Yeates, D. Cook); Mt Bellenden Ker, Summit, 1560m, beating foliage, (1 specimen, QMMO.14765, 1-7 Nov. 1981, Earthwatch/QM); Mt Bartle-Frere, NW-Centre Peak Ridge, 1400-1500m (1 specimen, QMMO.16125, 7-8 Nov. 1981, Earthwatch/QM); Mt Lewis, summit, 1200m (2 specimens, QMMO.15427, 9 Sept. 1981, G.B. Monteith, D. Cook); Mt Lewis, summit, 1200m, rainforest, stick brushings (1 specimen, QMMO.15433, 10 Sept. 1981, G.B. Monteith, D. Cook); Devil's Thumb area, 10km NW Mossman, rainforest (2 specimens, QMMO.15444, 9-10 Oct. 1982, G.B. Monteith, D. Yeates, G. Thompson); Mt Bellenden Ker, just below summit, approx. 1500m, under bark of rotting log, SMVFT (7 specimens, QMMO.14876, 4 Jul. 1983, J. Stanisic, D. Potter); Mt Bellenden Ker, summit TV str, 1560m, SMVFT (1 specimen, QMMO.11262, 25-31 Oct. 1981, Earthwatch/QM); Mt Bellenden Ker, summit TV str, 1560m, SMVFT, in axils of palm fronds (2 specimens, QMMO.11253, 17-24 Oct. 1981, Earthwatch/QM).

## Diagnosis

Shell large, diameter 5.62-7.15mm (mean 6.46mm), with 4  $\frac{3}{4}$  — 5  $\frac{1}{4}$  (mean 5-) normally coiled whorls. Apex and spire moderately to strongly elevated, body whorl not descending, spire protrusion about 2/5 body whorl width (Figs 2a-c). Height of shell 3.57-5.19mm (mean 4.35mm), H/D ratio 0.62-0.74 (mean 0.67). Apical sculpture of 17-20 prominent, narrow spiral cords. Protoconch of 1  $\frac{3}{4}$  whorls, 855µm in diameter at 1  $\frac{1}{2}$  whorls (Plate 1a-b). Post-nuclear whorls with widely spaced, strongly protractively sinuated radial ribs (Plate 1a), 49-83 (mean 70.9) on body whorl, whose interstices are 8-12 times their width. Ribs/mm 2.21-4.31 (mean 3.43). Microsculpture of numerous fine radial riblets, 6-10 between each pair of major ribs, crossed by fine, more closely spaced spiral cords (Plate 1c-d). Umbilicus narrow, reduced to a small chink in some individuals (Fig. 2c). Sutures simple. Whorls rounded above and below a broadly keeled periphery (Fig. 2b). Aperture sub-ovate, inclined about 25° from shell axis. Lip simple, parietal callus well developed (Fig. 2e). Colour yellow-horn to brown, with prominent (rarely reduced), red-brown flammulations, persisting on the base (Fig. 2a, c).

Description of Soft Parts — Foot and tail broad, bluntly rounded posteriorly, not tapering. Sole undivided, with strong transverse corrugations extending up the sides of the foot to the pedal groove. Pedal grooves high on foot, distinct, upper less prominent, uniting over tail. No mid-dorsal groove or caudal horn. Slime network well developed, irregular oblong to rectangular.

Body colour (in preservative) yellowy-brown, with pedal grooves, head region, mantle collar, posterior dorsal and lateral areas of foot covered by varying degrees of black pigmentation. Pallial roof with an arc of black pigmentation in heart region and variable spotting on left side behind the mantle collar. Ommatophores black.

Mantle collar (MC) thick, well developed, darkly pigmented in some specimens, glandular extension (MG) protruding onto anterior edge of pallial roof. Pneumostome (LP) obscured by mantle lobe (MA). Anus and pneumostome (LP) sharing a common opening to exterior. Anus opening just posterior to mantle collar with a narrow groove angling to exterior edge of mantle collar (Fig. 4c).

Pallial region long (almost  $\frac{7}{8}$  whorl apically), anterior edge with intrusive mantle gland (MG). Lung roof with varying degrees of black pigmentation, most notable overlying renal arm of the ureter (KD) and just posterior to mantle gland. Kidney (K) short, pericardial lobe vaguely triangular, rounded anteriorly and much longer than rectal lobe. Rectal lobe small, overlying hindgut (HG). Ureter (KD) sigmurethrous, secondary ureter absent. Ureteric opening (KX) just anterior to rectal arm of kidney. Heart (H) about  $\frac{2}{3}$  length of kidney. Principal pulmonary vein (HV) following contour of kidney to apex, then angled toward pneumostome, without conspicuous branches (Fig. 4c).



Ovotestis (G) embedded in apical coils of digestive gland, consisting of two clumps of palmately clavate alveoli orientated at right angles to plane of coiling (Fig. 4d). Apical clump variously sub branched. Clumps may be subdivided by digestive gland. Hermaphroditic duct (GD) large, swollen, iridescent pink and convoluted, sharply tapering at either end (Fig. 3d). Carrefour (X) a noticeable swelling at the base of the talon shaft, receiving a thin duct (Fig. 4b) from the ovotestis, a larger duct from the albumen gland (GG) and the slightly swollen stalk of the talon (GT). Talon a conspicuous swelling, embedded in the surface of albumen gland with a short, stout stalk which reflexes to enter the carrefour region (Figs. 3d, 4b). Prostate (DG) consisting of numerous acini, attached to one side of the uterus (UT) as a thin sheet for its entire length, then expanding into a bulbous mass at the level of the spermathecal head (Fig. 3d). Prostatic channel a lateral outpocket of the uterine lumen. Uterus (UT) superficially differentiated into two lower thick walled chambers and a thin walled upper chamber. Medial chamber brown in colour.

Vas deferens (VD) initially thickened then narrowed (Figs. 3a, 3c), descending vagina (V) to penioviducal angle, ascending penis (P) and entering epiphallus (E) at the level of the epiphallal caecum (ERC). Vas deferens — epiphallus region internally with simple longitudinal thickenings. Epiphallus with ascending and descending branches and very long (almost 4 times length of penis) epiphallal flagellum (EF) arising at the point of flexure and a short caecum (ERC) situated about  $\frac{1}{2}$  way along descending branch (Fig. 3c). Internally epiphallal caecum with walls thrown into folds, epiphallal flagellum with corrugated longitudinal pilasters. Epiphallus entering penis through a thickened pilaster (PV). Penis simple, muscularised tube, internally (Fig. 4a) with apical transverse pilasters (PP), longitudinal corrugated pilasters (PP), and a large central pilaster (PPM). Penial retractor muscle (PRM) short, inserted on the epiphallal caecum. Atrium (Y) short with longitudinal pilasters.

Free oviduct (UV) straight, long, almost equal in length to vagina. Vagina (V), internally with fleshy longitudinal pilasters, externally with prominent connective tissue (Fig. 3a). Spermatheca with a basal muscular portion, long convoluted stalk (SS) overlying uterus (Fig. 3a), and terminating in a sub-ovate shaped head (S) which lies in an area between the prostate and the albumen gland. Albumen gland (GG) a small roughly rounded mass of acini (Fig. 3b, d). (Based on 3 dissected specimens, QMMO.14876, QMMO.11253).

### Remarks

*Oreokera cumulus* (Odhner, 1917) has a disjunct distribution on the summits of the high peaks south of the Daintree River to Mt Bartle-Frere (Fig. 1). The distribution is unusual but can be related to recent regressions of rainforest habitat in the region caused by climatic change. The less elevated spire and subtle differences in shell features of the Black Mountain specimens would indicate that a study of interpopulational variation may be worthwhile in trying to understand possible speciation trends with the genus.

*O. cumulus* has a quite simple pattern of penial pilasters when compared with the actively speciating Pacific Island charopids. This may be related to its existence under fairly stable environmental conditions over a long period of time or a lack of sympatric relatives.

## OREOKERA NIMBUS SP. NOV.

Plate 2a-f; Figs 2d-f, 5a-f

### Comparative Remarks

*Oreokera nimbus* has a larger protoconch ( $1065\mu\text{m}$  at  $1\frac{1}{2}$  whorls) with more numerous and more closely spaced spiral striae than *O. cumulus*. In addition, the apical striae in *O. nimbus* are more 'squiggly' than in *O. cumulus* (Figs 2d-f, Plate 2a-b). Lack of adequate material does not make it possible to comment on differences in shape and coiling patterns between the two species. However, there are noticeable differences in the postnuclear microsculpture. The adult microsculpture of *O. nimbus* has the microspirals spaced as wide or wider than the radial riblets (Plate 2d) whereas in *O. cumulus* the microspirals are more closely spaced than the microradials (Plate 1c). Anatomically *O. nimbus* differs from *O. cumulus* in having a smaller epiphallal flagellum, more muscular and swollen penis with more complex internal pilasters, and a penial verge (Fig. 5a, 5d). The animal of *O. nimbus* appeared to be more darkly pigmented than *O. cumulus*, however, this may be individual rather than specific variation.



**Holotype**

QMMO. 16302, Thornton Peak, 11km NE Daintree, NEQ. Collected by G.B. Monteith, D. Yeates and G. Thompson 30 October, 1983. Height of shell 4.34mm, diameter 6.55mm, H/D ratio 0.66, whorls  $4\frac{3}{4}+$ .

**Paratypes**

Thornton Peak, 11km NE Daintree, NEQ, 1100-1200m (5 adults, 7 sub-adults and juveniles, QMMO. 15438, AMC.149590, 30 October, 1983, G.B. Monteith, D. Yeates, G. Thompson); Thornton Peak, NEQ, 1100-1300m (2 adults, 6 sub-adults and juveniles, QMMO.15170, 24-27 September, 1981, G.B. Monteith).

**Other Material**

Thornton Peak, NEQ, 1000-1300m (2 sub-adults, QMMO.15445, 20-22 September, 1981, G.B. Monteith, D. Cook); Thornton Peak, NEQ, summit, 1100-1300m, rainforest, sieved litter and moss (1 sub-adult and 1 juvenile, QMMO.16304, 24-27 September, 1984, G.B. & S.R. Monteith).

**Diagnosis**

Shell large, 5.62-6.55mm (mean 6.08mm) in diameter, with  $4\frac{1}{2}$ - $5\frac{1}{8}+$  (mean  $4\frac{3}{4}+$ ) normally coiled whorls. Apex and spire strongly elevated, body whorl not descending (Fig. 2d-f). Height of shell 3.92-4.43mm (mean 4.26mm), H/D ratio 0.66-0.75 (mean 0.70). Apical sculpture of 24-30 prominent spiral cords which are initially regular then becoming noticeably squiggly or zig-zagged (Plate 2b). Protoconch of  $1\frac{1}{4}$  whorls, 1065µm in diameter at  $1\frac{1}{2}$  whorls (Plate 2a). Postapical whorls with widely spaced, strongly protractively sinuated radial ribs, 54-73 (mean 63) on body whorl, whose interstices are 8-12 times their width (Plate 2c). Major ribs with well developed periostracal blades. Ribs/mm 2.92-3.79 (mean 3.28). Microsculpture of numerous fine radial riblets, 6-13 between each pair of major ribs, crossed by fine, more widely spaced spiral cords (Plate 2d). Sculpture not reduced below periphery and continued on base (Plate 2f). Umbilicus narrow, reduced to a lateral crack in some individuals (Fig. 2f). Sutures simple. Periphery broadly keeled (Fig. 2e). Aperture sub-ovate inclined about  $25^\circ$  from shell axis. Lip simple, parietal callus well developed. Colour brown with prominent red-brown flammulations, persisting on base (Fig. 2d, 2f). Based on 7 measured adults.

**Description of Soft Parts** — Foot and tail broad, bluntly rounded posteriorly. Sole undivided with very strong transverse corrugations extending up the sides of the foot to the pedal groove. Pedal grooves high on foot, distinct, upper less prominent, uniting over tail. No mid-dorsal groove or caudal horn. Slime network well developed, irregularly oblong to rectangular.

Body colour (in preservative) yellowy-white, with pedal glands, head region, mantle collar, posterior dorsal and lateral areas of foot, distinctively dark grey to black. Pallial roof with a large area of black pigmentation. Ommatophores black.

Mantle collar (MC) not as well developed as in *O. cumulus*, with mantle gland (MG) only slightly intruding onto pallial roof. Pneumostome (LP) obscured by mantle lobe (MA). Anus and pneumostome sharing a common opening to the exterior. Anus opening just posterior to mantle collar (Fig. 5f).

Pallial region contracted, anterior edge with slight intrusion of mantle gland (MG). Lung roof with a large area of black pigmentation in the anterior half. Kidney (K) short, pericardial lobe vaguely triangular, reflexed away from the rectum (HG), rounded anteriorly and much longer than rectal lobe. Rectal arm of kidney reduced to a small knob of tissue overlaying rectum (HG). Ureter (KD) sigmoid, without secondary branch. Ureteric opening (KX) just anterior to rectal kidney arm. Heart (H) about  $\frac{2}{3}$  length of kidney, principal pulmonary vein (HV) not branched (Fig. 5f).

Ovotestis (G), two clumps of palmately clavate, white alveoli, embedded in the pink apical whorls of the digestive gland (Z). Apical clump larger and separated from subapical clump by digestive gland tissue (Fig. 5e). Hermaphroditic duct (GD), light iridescent pink and strongly kinked (Fig. 5c). Carrefour (X) not seen. Talon (GT) a subcircular swelling embedded in the surface of the digestive gland, with a short stout stalk which reflexes to enter the carrefour region (Fig. 5b). Prostate (DG) white, consisting of numerous acini arranged as a thin sheet of tissue on the lower uterine chamber, expanding into a bulbous mass at the level of the albumen gland (GG). Uterus (UT)

too flattened to observe differentiation, central region brown in colour. Albumen gland, a roughly rounded mass of acini, deformed by contraction. Spermatheca (S) with a muscularised basal portion (Fig. 5a), gradually tapering to a thin stalk (SS), terminating in a sub-ovate head lying at the base of the albumen gland.

Vas deferens (VD) initially thickened then descending to penioviducal angle, ascending penis (P) and entering epiphallus at the level of the epiphallal caecum (ERC). Epiphallus (E) reflexed, with ascending and descending branches (Fig. 5a). Long (about 2 times length of penis) epiphallal flagellum (EF) arising at the point of flexure. Small epiphallal caecum (ERC) about midway along descending section of epiphallus (Fig. 5a). Penial retractor muscle (PRM) very short, inserting on the caecum (Fig. 5b, 5d).

Epiphallus, vas deferens and flagellum internally with longitudinal pilasters. Penis (P) muscularised and swollen apically, internally (Fig. 5d) with large, corrugated longitudinal pilaster (PPM), a pocket stimulator (PPS) and wall sculpture of low corrugated pilasters (PP). Epiphallus (Fig. 5d) enters penis apically through two thickened pilasters which function as a verge (PV). Apicad of verge, epiphallus with two large thickened longitudinal pilasters (EPP).

Free oviduct (UV) short (Fig. 5a), contracted, almost as long as vagina (V). Vagina internally with thin, longitudinal pilasters, externally with pigmented connective tissue (Fig. 5a). Atrium (Y) short with internal longitudinal pilasters. Based on one dissected adult. (QMMO.15438).

TABLE 2. Variation in *Oreokera nimbus*

LOCALITY	NUMBER OF ADULTS MEASURED	RIBS ON BODY WHORL	RIBS PER MM	HEIGHT (MM)	DIAMETER (MM)	H/D	WHORLS
Thornton Peak	7	63	3.28	4.26	6.08	0.70	4¾+
QMMO.16302		(54-	(2.92-	(3.92-	(5.62-	(0.66-	(4½-
QMMO.15438		73)	3.79)	4.43)	6.55)	0.75)	5½+)
AMC.149590							

### Remarks

*Oreokera nimbus* is known only from the summit (alt. approx. 1000m) of Thornton Peak (Fig. 1). Even though the geographic distance is no greater than that shown by the north-south range of *O. cumulus*, it has not been found on neighbouring Mt Hemmant (1092m) and Mt Pieter Boite (1046m) or the more northerly Mt Finnegan (1148m).

Monteith (1985) noted that the Mt Sorrow Tableland which includes the slopes of Mt Pieter Boite, lacked many of the insect taxa found on the Bellenden Ker Range. However, it did contain some relict endemic taxa. He suggested that while these facts established the area as a refuge zone, it may have been less significant than some of the higher massifs in the south. Hence, the absence of *Oreokera* on some of the more northern peaks of the Daintree-Helenvale rainforest may in fact be related to biogeographical factors and not to the vagaries of collecting effort.

*O. nimbus* has more specialised protoconch sculpture and penial pilaster patterns than *O. cumulus*. These changes are related to species recognition and indicate a separation earlier than that responsible for the disjunct distribution of *O. cumulus*.

*Oreokera nimbus* is sympatric with a number of other undescribed charopids but is easily distinguishable by its elevated spire and large size.

The name *nimbus* refers to occurrence of this species on the often cloud enshrouded summit of Thornton Peak and its popular association with *cumulus*.



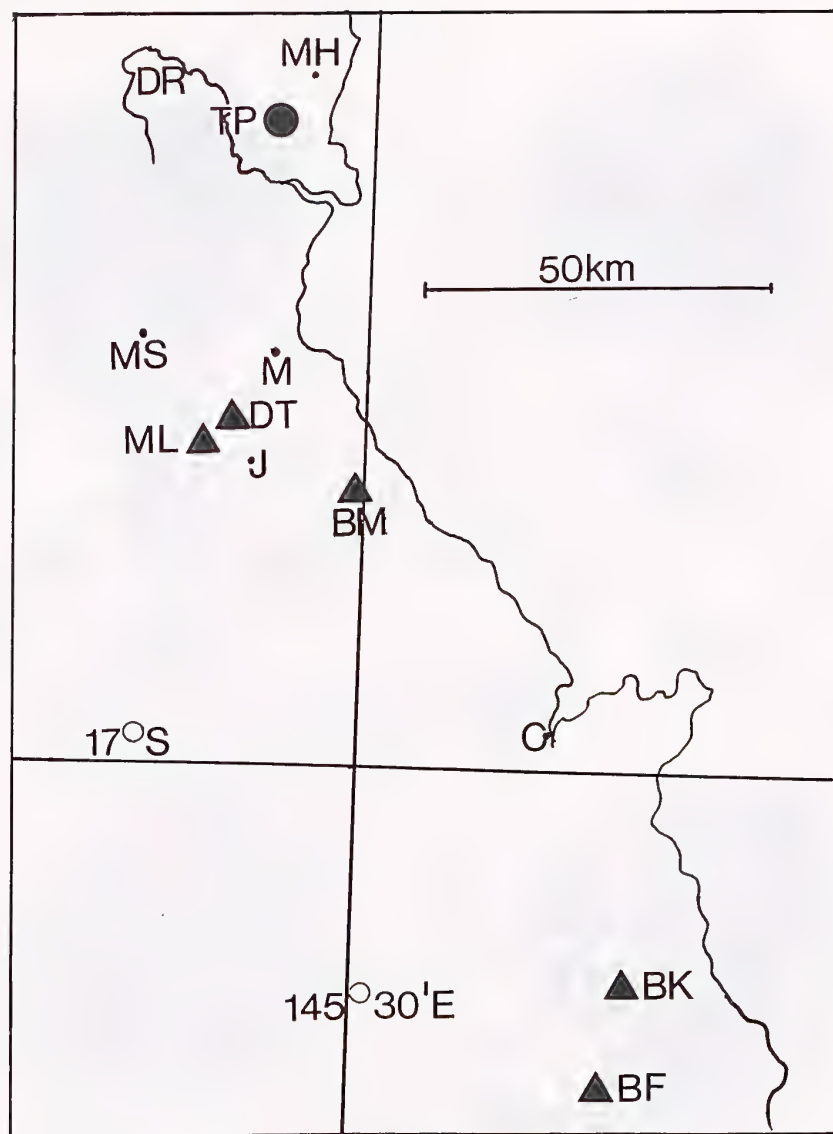


FIGURE 1. Distribution map of *Oreokera cumulus* (black triangles) and *Oreokera nimbus* (black dot) with major landmarks shown.

LEGEND: BF = Mount Bartle-Frere; BK = Mount Bellenden Ker; BM = Black Mountain; C = Cairns; DR = Daintree River; DT = Devil's Thumb; J = Julatten; M = Mossman; ML = Mount Lewis; MH = Mount Hemmant; MS = Mount Spurgeon; TP = Thornton Peak. (Scale as marked.)

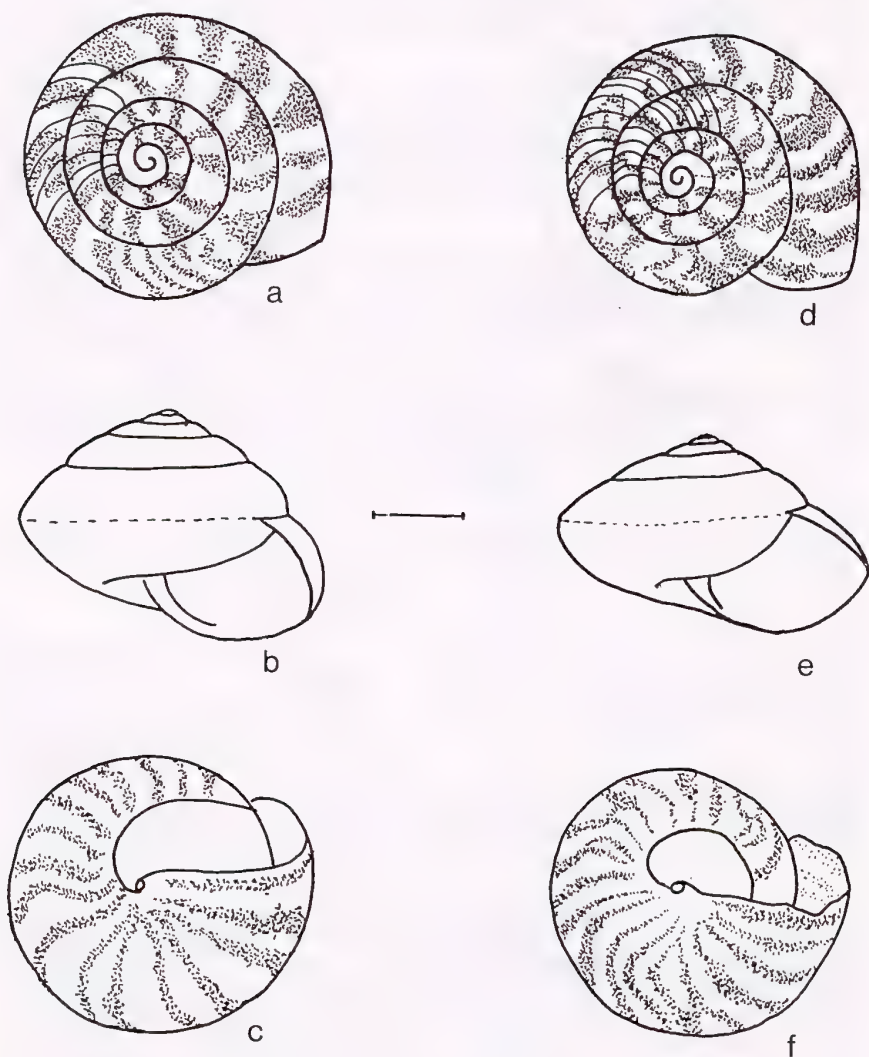


FIGURE 2. Shells of *Oreokera*. (a-c) *Oreokera cumulus* (Odhner, 1917), Mt Bellenden Ker, 1-7 Nov. 1981, QMMO.14765; (d-f) *Oreokera nimbus*, Thornton Peak, 30 Oct. 1983, QMMO.16302, holotype. (Scale line = 2mm.)



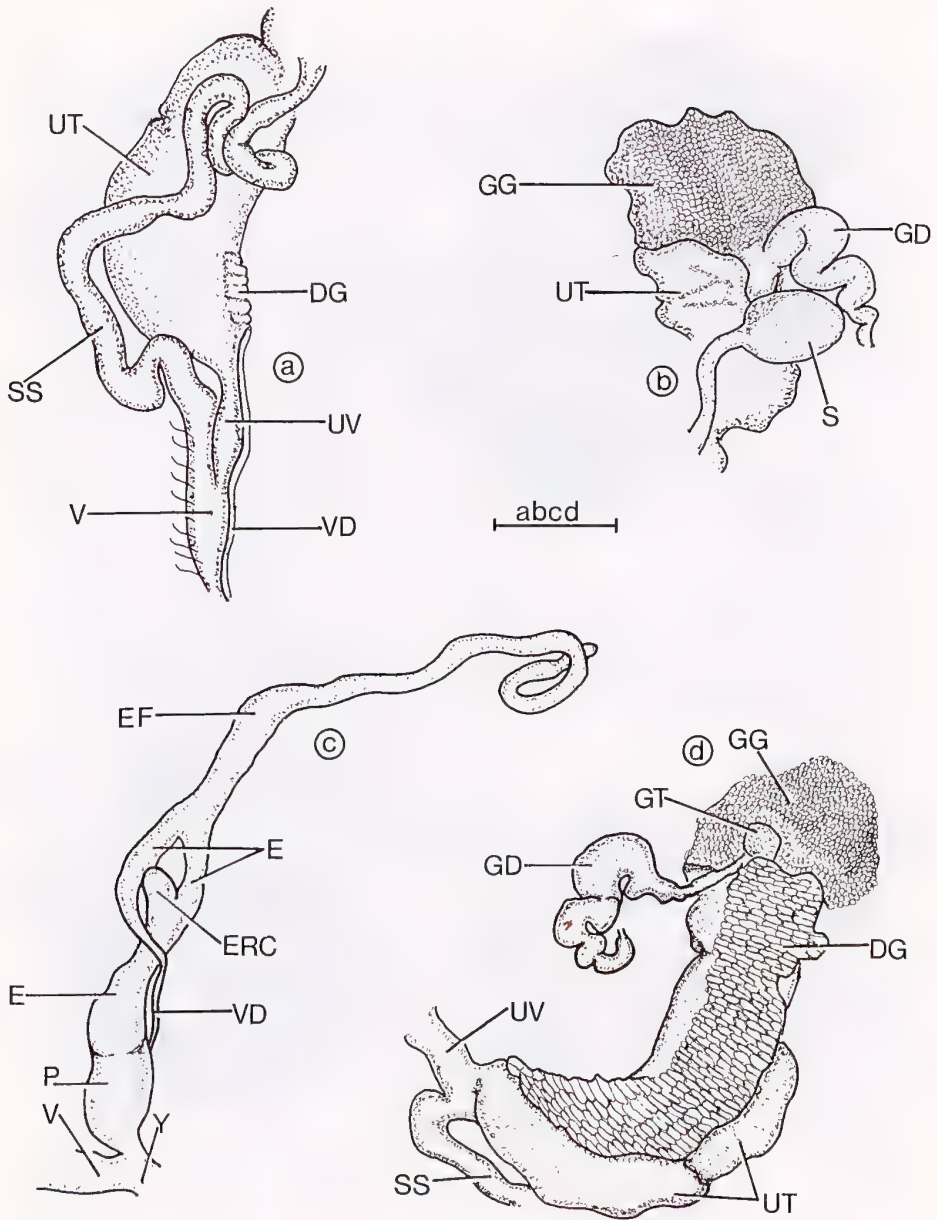


FIGURE 3. Genitalia of *Oreokera cumulus* (Odhner, 1917), Mt Bellenden Ker, 4 Jul. 1983, QMMO.14876; (a) lower female tract; (b) albumen gland, spermatheca and hermaphroditic duct; (c) lower male tract; (d) utero-prostate. (Scale line = 1mm.)

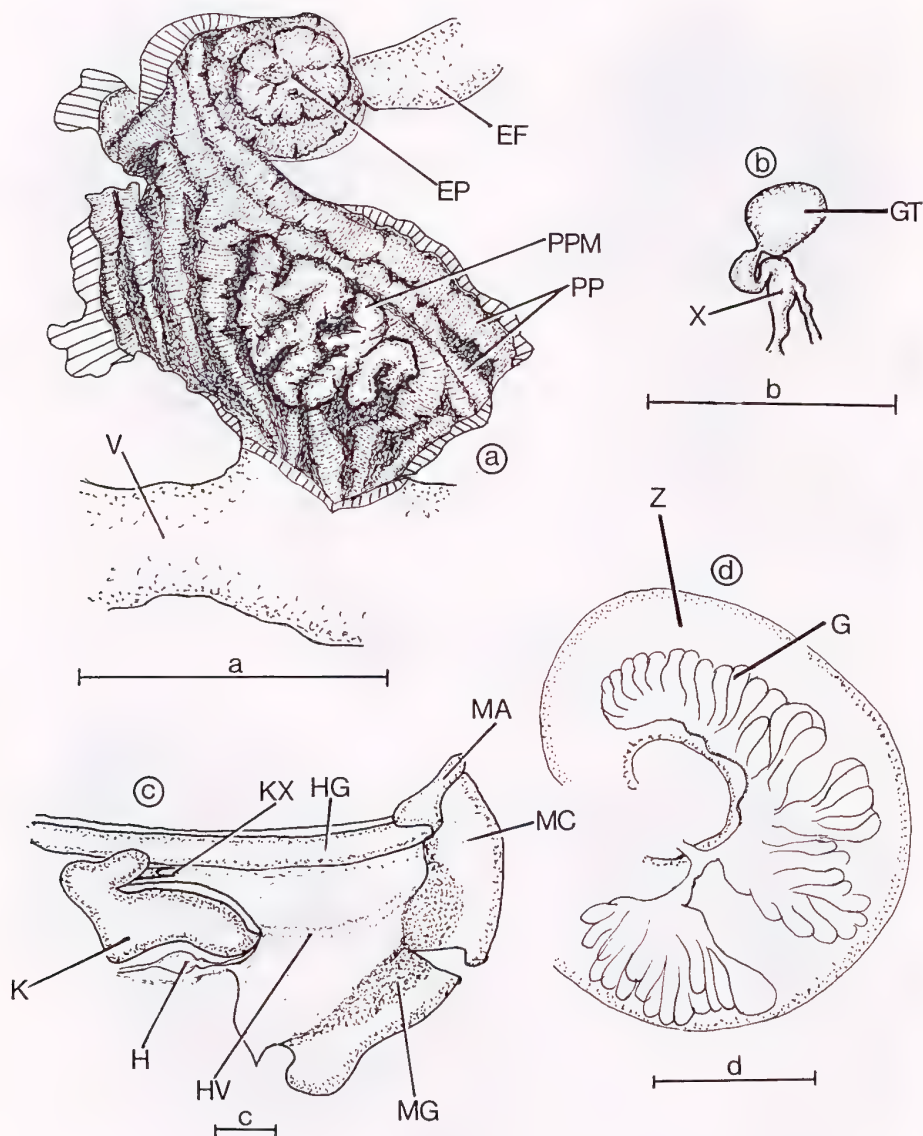


FIGURE 4. Genitalia of *Oreokera cumulus* (Odhner, 1917), (a) Mt Bellenden Ker, 17-24 Oct. 1981, QMMO.11253; (b-d) Mt Bellenden Ker, 4 Jul. 1983, QMMO.14876. (a) penis interior; (b) talon and carrefour; (c) pallial cavity; (d) ovotestis. (Scale lines = 1mm.)



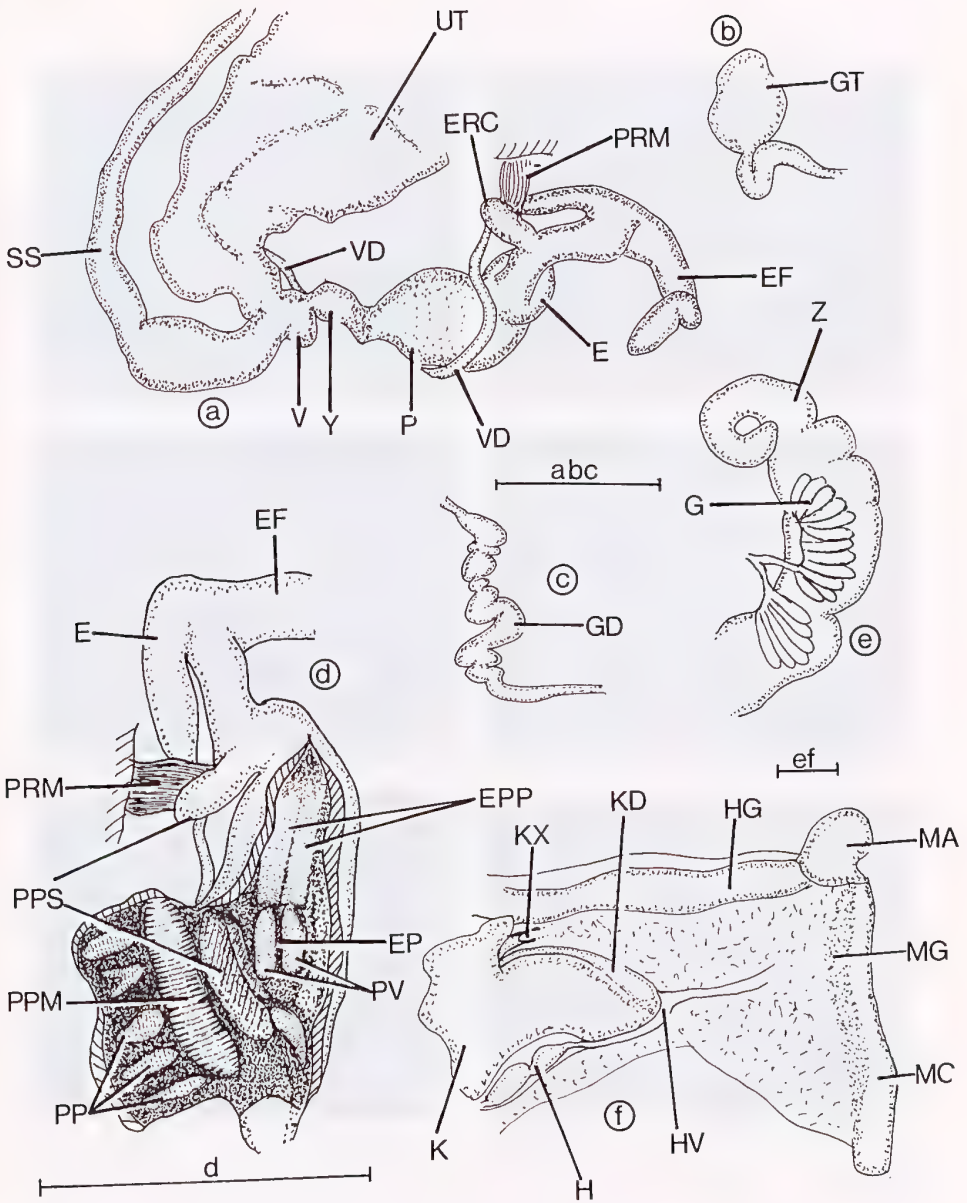
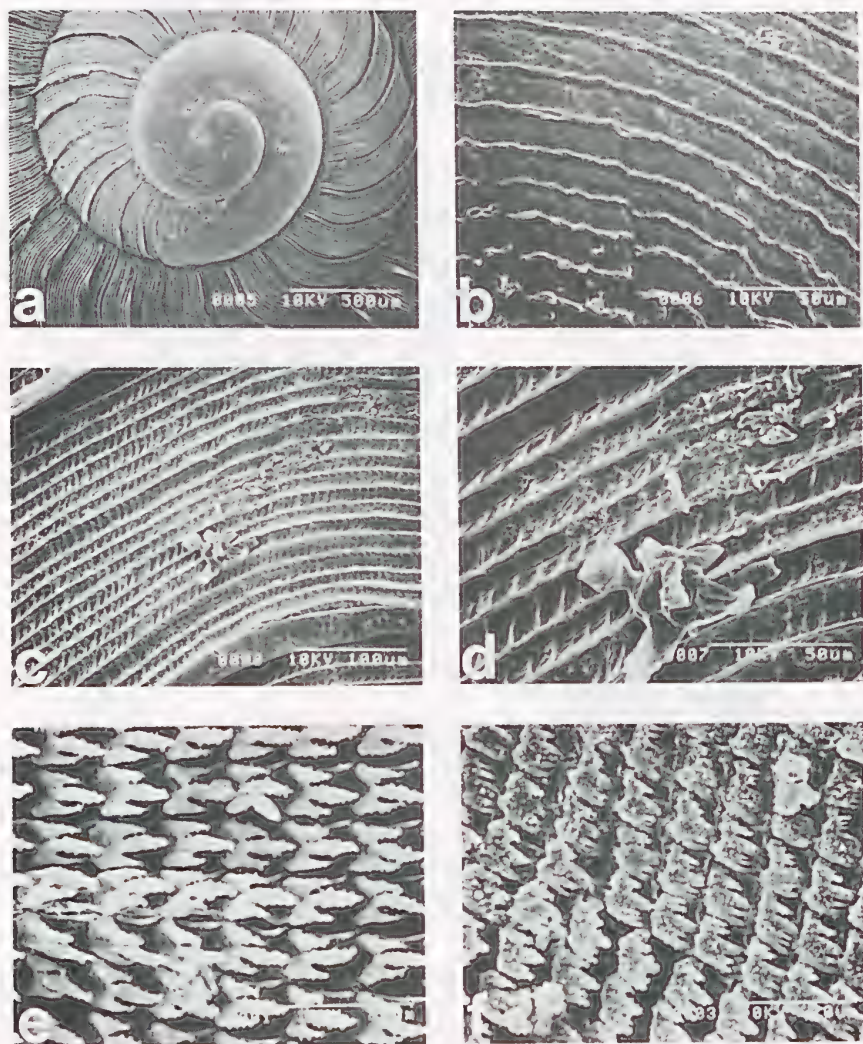


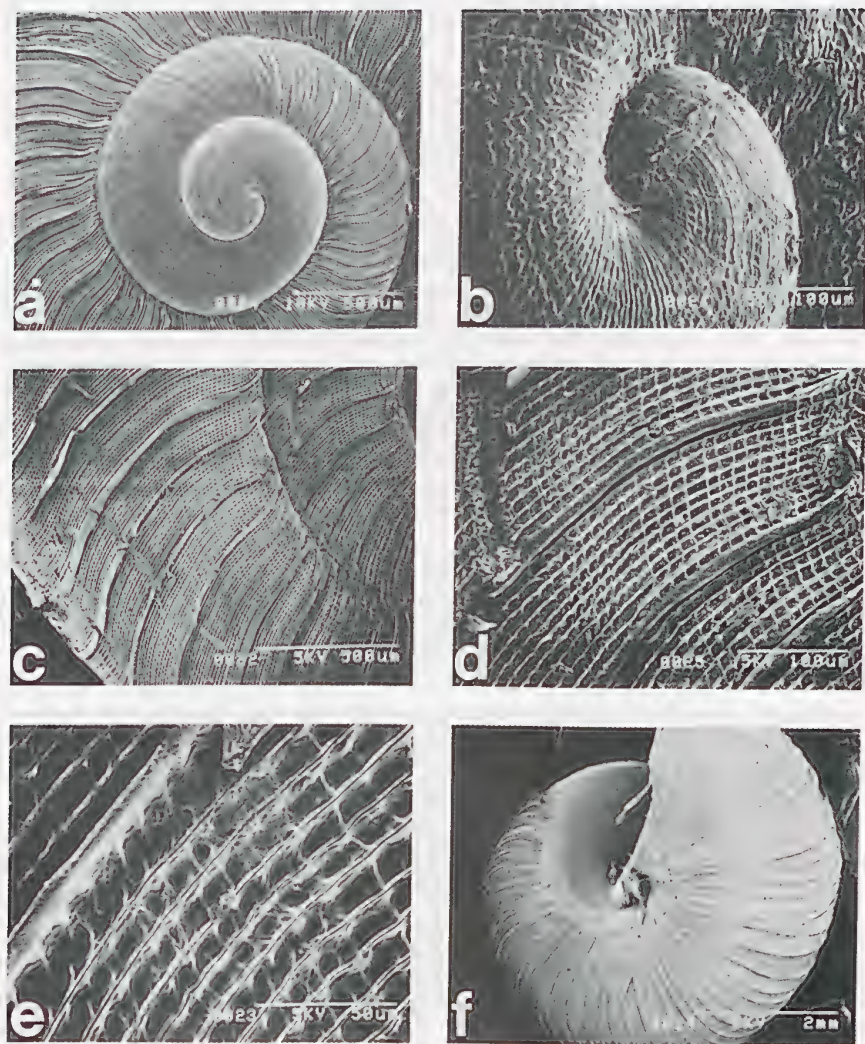
FIGURE 5. Genitalia of *Oreokera nimbus*, Thornton Peak, 30 Oct. 1983, QMMO.15438, paratype. (a) terminal genitalia; (b) talon; (c) hermaphroditic duct; (d) penis interior; (e) ovotestis; (f) pallial cavity. (Scale lines = 1mm.)



# PLATE 1

Shell sculpture and radula of *Oreokera cumulus* (Odhner, 1917), (a-d) Mt Lewis, 9 Sept., 1981, QMMO.15427; (e-f) Mt Bellenden Ker, 4 Jul. 1983, QMMO.14876. (a) apical region; (b) close up of apical cords; (c) microsculpture of first adult whorl; (d) detail of adult microsculpture; (e) central and lateral teeth; (f) marginal teeth. (Scale lines as shown.)





# PLATE 2

Shell sculpture of *Oreokera nimbus*, (a) Thornton Peak, 30 Oct. 1983, QMMO.15438, paratype; (b-f) Thornton Peak, 24-27 Sept. 1981, QMMO.15170. (a) apical region: (b) detail of apical cords; (c) adult sculpture; (d) microsculpture on first adult whorl (e) detail of adult microsculpture (f) basal view. (Scale lines as shown).

## DISCUSSION

### Comparative Analysis of *Oreokera* Patterns

The charopid fauna of tropical and sub-tropical eastern Australia is largely undescribed, while the known taxa of south-east Australia await detailed anatomical study and generic revision. Hence, only a gross outline of the relationships of *Oreokera* can be given at this stage.

Of the recently reviewed Australian taxa (Solem, 1983, pp. 74-81; Solem, 1984; Smith and Kershaw, 1985) only the widespread, minute species, *Discocharopa aperta* (Mollendorff, 1894), and three species from Victoria and Tasmania, *Thyrasona diemenensis* (Cox, 1868), *Stenacapha hamiltoni* (Cox, 1868) and *Mulathena fordei* (Brazier, 1871) are known from soft parts. Two further species *Dupucharopa millestriata* (Smith, 1894) and *Pilsbrycharopa tumidus* (Odhnér, 1917), were reviewed known from shells only (Solem, 1984).

In having a much reduced rectal lobe of the kidney (Figs 4c, 5f), *Oreokera* is similar to the widespread *D. aperta* and readily distinguished from the endemic Pacific Island taxa in which the kidney lobes are either equal to subequal in length or the pericardial lobe is significantly shorter (Solem, 1983, pp. 31-32). The New Zealand charopid *Phenacohelix pilula* (Reeve, 1852) and some other east Australian species (Stanisic, unpublished) show similar renal configurations. This feature is also shared with the South American species, *Stephanoda binneyana* (Pfeiffer, 1847). The degree of relationship indicated by this shared character is difficult to assess. Certainly in the case of *D. aperta* the many differences in shell and anatomy between it and *O. cumulus* do not suggest a close relationship. *D. aperta* has a minute white shell with depressed apex, wide umbilicus, reduced whorl count, radially sculptured protoconch and reduced to absent postnuclear spiral microsculpture. Anatomically *D. aperta* has no accessory appendages on the male genitalia, displays sub-apical insertion of the vas deferens, a finger-like talon and more significantly a complete secondary ureter.

Unfortunately, Smith and Kershaw (1985) did not give details of the pallial configurations of *Mulathena fordei*, *Stenacapha hamiltoni* and *Thyrasona diemenensis*, nor did they present some essential fine detail of their reproductive anatomy. While these factors restrict the nature of comparative remarks, sufficient gross differences exist between these taxa and *Oreokera* to indicate strong generic differentiation.

Conchologically, the major difference between *Oreokera* and these species is in the sculpture of the protoconch. The nuclear whorls of *Oreokera* have numerous low, regular to irregular spiral cords (mean 23) whereas *M. fordei*, *S. hamiltoni* and *T. diemenensis* have reticulately sculptured protoconchs in which radial elements predominate and spiral cording may be reduced or absent. Solem (1970, p.262) regarded spiral apical cording in the Charopinae as a primitive condition. It is much more widespread among Pacific Island groups, including the New Caledonian genus *Andrefrancia* Solem, 1960 than Austrozealandic taxa in which patterns of protoconch sculpture show numerous modifications of the three basic patterns — spiral, radial and reticulate.

*Pilsbrycharopa tumidus* (Odhnér, 1917) from the Northern Territory and *Dupucharopa millestriata* (Smith, 1894) from Western Australia show basic departures from *Oreokera* in patterns of protoconch sculpture which highlight the level of experimentation in this feature among Australian taxa. *P. tumidus* has complex apical sculpture consisting of a series of regularly arranged pits while *D. millestriata* has widely spaced radial ribs crossed by unbroken spirals (Solem, 1984).

Among the described sub-tropical and tropical species with spirally lirate protoconchs, *Setomedea seticostata* (Hedley, 1924) from north-east New South Wales and south-east Queensland differs from *O. cumulus* in having a more tightly coiled shell with flattened spire and regularly arranged periostracal setae. *Roblinella disjuncta* Iredale, 1941 from Byron Bay in north coastal New South Wales has a tightly coiled shell with depressed spire, wide umbilicus and poorly defined adult microsculpture. '*Roblinella*' *intermedia* (Odhnér, 1917) from North Queensland was incorrectly assigned by Iredale (1937) who believed it had a spirally striate protoconch when in fact the nuclear whorls have strongly reticulate sculpture.

The postnuclear sculpture of *O. cumulus* is typically charopid (Plates 1a, c-d, 2a, c-e) and shows basic consistencies with other Australian and extralimital taxa in having a pattern of primary radials



with a microsculpture of fine radial riblets and spiral cords. However, without adequate scanning electron microscope (hereafter SEM) studies, it is difficult to make meaningful comparisons. Solem (1976, 1983) has shown that optically similar sculpture in the Charopidae and Endodontidae may often be based on quite different microstructure which is only visible through SEM. The New Zealand species *Paracharopa chrysaugaeia* (Webster, 1904) and two congeners *P. goulstonei* Climo, 1983 and *P. fuscata* (Suter, 1894) display postnuclear sculpture in which the major ribs develop strong periostracal elements similar to that seen in *O. cumulus*. However these species have quite different patterns of shell shape and highly modified nuclear sculpture. (Climo, 1983). This similarity in sculptural pattern may have a purely functional basis as *P. chrysaugaeia* has similar microhabitat requirements to *Oreokera* i.e. under bark of trees.

Anatomically *Oreokera* is distinguished from other Australian, New Zealand and Pacific Island charopids by the presence of two accessory appendages on the male genitalia (Figs 3c, 5a) and lack of a secondary ureter (Figs 4c, 5f). *Mulathena fordei* and *Stenacapha hamiltoni* both lack either an epiphallal flagellum or caecum. *M. fordei* has no externally differentiated epiphallus while *S. hamiltoni* has a simple epiphallus with more swollen penis. On the other hand *Thyrasona diemenensis* does possess an epiphallal caecum. Significantly this occurs at the vas deferens — epiphallus junction and apical of the penial retractor muscle insertion. Hence, allowing for the lengthened epiphallus in *Oreokera* this structure corresponds positionally to the flagellum in *Oreokera*. But while Smith and Kershaw (1985) considered the presence of an epiphallal caecum in *Thyrasona* Smith and Kershaw, 1985 as a diagnostic feature, the phylogenetic significance of accessory genital structures in the Charopidae is difficult to interpret at this stage. The New Guinea species *Pilsbrycharopa gressitti* Solem, 1970 and *Paryphantopsis dauloensis* Solem, 1970 possess epiphallal diverticula and Solem (1970, p. 263) considered this a major departure from the pattern in Pacific Island charopids. However, both *Pilsbrycharopa* Solem, 1958 and *Paryphantopsis* Thiele, 1928 show a number of basic conchological and anatomical differences from *Oreokera* suggesting that possession of these accessory structures among non-Pacific Island species may be convergent. New Zealand taxa also show some development of accessory appendages but in contrast to *O. cumulus* these diverticula are all penial. Nevertheless, their occurrence in such diverse species as *Maoriconcha oconnori* (Powell, 1941), *Charopa colensoi* (Suter, 1890), *Phenacharopa novoseelandica* (Pfeiffer, 1853) and *Otoconcha roscoei* Climo, 1971 again suggests that they have no phyletic significance (see Climo, 1969, 1970, 1971).

Solem (1983) gives detailed accounts of the variation in the genitalia of 43 species level taxa of Pacific Island Charopidae. *Oreokera* shows significant departures from the basic patterns exhibited by these taxa. The enlarged ovotestis with nearly right angle orientation, strongly kinked hermaphroditic duct, accessory male appendages and epiphallal insertion of the penial retractor muscle (Figs 3c-d, 4d, 5a) all effectively delineate *Oreokera* from the Pacific Island species. Thus while there are some broad conchological similarities between *Oreokera* and the Pacific Island groups, anatomical differences are sufficient to suggest that these consistencies are a result of parallel evolution over a long period rather than recent common ancestry.

Anatomical similarities do exist between *Oreokera* and some New Zealand taxa. *Thalassohelix propinqua* (Hutton, 1883) has a very similar ovotestis configuration while *Allodiscus dimorphus* (Pfeiffer, 1853) and *Flammulina zebra* (le Guillou, 1812) display kinking of the hermaphroditic duct. In each of these cases however, the features mentioned are the result of secondary modifications due to experiments in visceral hump reduction (*F. zebra*) or size increment (*T. propinqua* and *A. dimorphus*).

*Oreokera* has an increased whorl count (mean 4 $\frac{7}{8}$ –) and size (mean diameter 6.36mm) when compared with Pacific Island species (median mean whorl count 4 $\frac{1}{8}$ –, median mean diameter 2.76mm). It also has increased spire height (Figs 2b, e) associated with the ecological shift to arboreal existence. Hence, the 'radical' patterns seen in the genitalia may be related to associated visceral hump elongation. Certainly the ovotestis orientation and kinked hermaphroditic duct have parallels among large New Zealand species. The lengthening of the epiphallus with the addition of a caecum and extra long flagellum may also be secondary changes associated with the increased shell size and height. That all organs are not involved in this elongation is of no real consequence. Solem (1976, p. 95; 1983, p. 37) has demonstrated that visceral hump compaction or elongation proceeds

on a zonal basis with regard to the organs involved. In this case the elongation has occurred in the 'subterminal' genitalia with no equivalent change in the penis, vagina or pallial gonoducts.

At odds with these seemingly coherent habitat-shift changes are the prominent post nuclear sculpture and conservative foot structure of *Oreokera*. Solem (1976, 1983) found that the larger arboreal and semi-arboreal endodontoid taxa of the Pacific Islands showed reduction or loss of shell sculpture! By way of contrast, Solem and Climo (1985, p. 25) found that New Zealand taxa did not show any correlation between sculptural prominence and habitat. In this respect *Oreokera* fits the New Zealand pattern. The absence of any foot specialisation contrasts with the caudal horn and foss developed in many arboreal New Zealand taxa and may indicate recent utilisation of the arboreal niche under different evolutionary circumstances.

In spite of the many similarities between *Oreokera* and other charopids in the Austrozealandic and Pacific areas, the one feature which distinguishes it from all these taxa is the absence of a secondary ureter (Figs 4c, 5f). Solem (1976, p. 84-87) considered the closed secondary ureter in the Charopidae as a derived condition whose functional significance was largely responsible for the greater evolutionary success of the Charopidae in exploiting habitats where water loss would present a major problem. Hence the Charopidae have had success in arboreal and semi-arboreal situations, survived in desert conditions and produced several lineages of slug-like taxa.

While some Rotadiscinae e.g. *Radiodiscus batricolus* (Guppy, 1868) from Central America (see Baker, 1927, p. 23) have partially complete secondary ureters the absence of a secondary ureter has to my knowledge only been definitely recorded in one other charopid, namely, the Juan Fernandez Island species, *Amphidoxa marmorella* (Pfeiffer, 1845). On the other hand it is the typical condition in the Pacific Island Endodontidae.

Whether or not this entitles *Oreokera* to subfamilial recognition must wait until further studies on the Australian and New Zealand species are completed.

At present the difficulties lie with interpreting the basic patterns to which *Oreokera* should be compared. However, if one accepts the changes which may be due to habitat shift (ovotestis orientation, kinked hermaphroditic duct, epiphallidic flagellum and caecum) and those due to species recognition (modified penial pilaster in *O. nimbus*) then the absent secondary ureter, simplified penial pilaster in *O. cumulus* and spiral cording of the protoconch represent a mosaic pattern of primitive characters which may have given rise to the more specialised Charopinae of the Austrozealandic and Pacific Island regions.

### Biogeography

The range of *Oreokera* forms part of the largest continuous area of rainforest in Australia. However the actual distribution of the genus encompasses only a select few of the many different structural types of closed forest which combine to make up this rainforest massif. *O. cumulus* and *O. nimbus* are restricted to altitudes above 1000m, and while this may seem unusual, it is a characteristic shared with a number of other biogeographically significant organisms found within this region (see Monteith, 1980).

The humid tropical region of north-east Queensland (lat. 15°-19°S, long. 145°-146°30'E as defined by Tracey, 1982) includes the highest mountains of northern Australia. These mountains (Mt Bartle-Frere, Mt Bellenden Ker, Thornton Peak, etc.) are batholithic granite intrusions of Permian origin, which have become gradually exposed by the erosion of overlying strata. Although not particularly high, the change in altitude from sea level to over 1600m is sufficient to produce a range of microclimates which together with local variation in topography and soil types have led to considerable altitudinal variation in the plant and animal communities existing on these peaks.

Tracey and Webb (1975) mapped the vegetation of the region and showed that the granites and schists of the cloudy wet highlands (greater than 1000m in altitude) supported quite different plant communities to the complex mesophyll vine forests found on the largely basaltic, wet to very wet lowlands and foothills. They recognised two structural types of rainforest at altitudes above 1000m. These were simple microphyll vine fern forest (hereafter SMVFF) and, near the summit, simple microphyll vine fern thicket (hereafter SMVFT). The SMVFT and to a lesser extent SMVFF contain a number of relict plant and animal taxa whose biogeographic status belies the altitudinal



progression of vegetation types from complex to simple. The presence in these montane environments of relict floristic elements such as *Rhododendron lochae*, *Dacrophyllum sayeri*, *Orites* sp. and *Agapetes* sp. attests to their status as major refugia during the Tertiary when many mesic communities underwent large scale attrition (Webb and Tracey, 1981, p. 654).

Kikkawa, Monteith and Ingram (1981, pp. 1707-1712) provide numerous examples of insects which are confined to these refugia. They include both Gondwanic relicts such as flightless dung beetles of the genus *Ignambia* with congeners in New Caledonia and the stag beetle *Sphaenognathus queenslandicus* Moore, 1978, from a genus only otherwise known from South America, as well as autochthonous elements which include the flightless pterostichinine carabid beetles of Darlington (1961a,b,c) and the flightless aradid hemipterans of the genus *Kumaressa* (see Monteith, 1980). These examples highlight the great antiquity of the refugia on the one hand and their role as epicentres of internal evolution on the other. Floristically the situation is analogous with primitive angiosperms and narrow endemics characteristic.

It is in this context that *Oreokera* must be viewed.

With a combination of altitudinally restricted disjunct distribution and primitive characters, *Oreokera* is very much part of this unusual suite of relictual organisms. Monteith (1980) provides a useful summary of some of the non-molluscan elements. In the case of *Oreokera*, its present distribution can best be explained by the fragmentation of a much wider distribution due to habitat regression caused by intermittent episodes of aridity since the mid to late Tertiary. Kershaw (1980) has detailed the chronology of climate induced changes of rainforest communities in the north and has shown that even quite recently (8000 B.P.) there have been major altitudinal shifts of the plant communities in this region. In particular there is evidence to suggest that the present microphyll vine forests of the summits and near summits existed at much lower altitudes in the past when conditions were moister.

*Oreokera* would certainly have had a more widespread distribution in the past, but is now restricted to the mountain top refugia which ensured its survival through the Tertiary.

It is highly probable that the circumscribed distribution of *Oreokera* in time and space is related to its lack of a water conserving secondary ureter. Solem (1976, p. 100) identified the lack of a secondary ureter in the Pacific Island Endodontidae as a major reason for their restriction to areas of high humidity levels. The lack of a closed secondary ureter necessitates the use of water stored in the pallial cavity to help flush out excretory products. This water loss is a significant problem for small snails. As its moist habitat regressed into mountain top refugia at various times throughout the Tertiary so did *Oreokera*. At present the habitat type is in regression and if this should last for some considerable time then the tendency for the isolated populations of *Oreokera cumulus* (Odhner, 1917) to speciate under localised environmental changes, will increase.

Additionally, the presence of a closed secondary ureter in the Charopidae is considered to be an important factor in the ability of its members to exploit the less humid arboreal and semi-arboreal niches (Solem 1976, 1983). The exceptional case of *Oreokera* (arboreal existence and lack of a secondary ureter) does have analogs within the Endodontidae. Solem (1976, p. 100) reports that species of *Cookeconcha* are found on dead stumps and logs, and under the bark of dead trees. Furthermore, the Tahitian species *Libera bursatella* (Gould, 1846) was taken in the axils of *Freycinetia* at 4700-5000ft elevation. In each case however, the water conservation problem was minimised by high (4375-5000mm/year) rainfall. Thus while *Oreokera* is moist adapted and environmentally restricted, the rainfall is high enough (approx. 5000-6250mm/year) to allow it to exploit niches above the ground stratum. Furthermore, the refugia to which *Oreokera* is now confined would have provided the long term environmental stability necessary for the preservation of this primitive character.

*Oreokera nimbus* represents an early separation from the antecedent of *O. cumulus*. The vicariant event responsible for this separation was most likely the formation of the Daintree River. Hence *O. nimbus* would have been effectively isolated from even quite recent episodes of rainforest expansion which would have seen present montane refugial communities existing at much lower altitudes and favouring the continued mixing of the *O. cumulus* populations.

The relationships of *Oreokera* remain to be determined, but it would not be surprising to find that these lie with charopids much further south or even in places such as Lord Howe Island, New Caledonia, New Zealand or perhaps South America.

## CONCLUSIONS

*Oreokera cumulus* and *Oreokera nimbus* are ancient relicts which preserve a mosaic of primitive characters. The lack of a secondary ureter in *Oreokera* makes it unique among the Austrozealandic Charopidae and distinguishes it as a taxon with features from which the more specialised Charopidae could have evolved. However, only when further studies on other species in Australia and New Zealand are completed will the implications of this discovery become fully known.

The present distribution of the genus and the events leading to the existence of two species — one widespread and one localised — are inextricably linked to the existence of the montane refugia in which northern mesic communities have managed to persist throughout the climatic vicissitudes of the mid to late Tertiary.

## ACKNOWLEDGEMENTS

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## APPENDIX

### List of Anatomical Abbreviations

DG, prostate; E, epiphallus; EF, epiphallic flagellum; EP, epiphallic pore; EPP, epiphallic pilaster; ERC, epiphallic retractor caecum; G, ovotestis; GD, hermaphroditic duct; GG, albumen gland; GT, talon; H, heart; HG, hind gut; HV, principal pulmonary vein; K, kidney; KD, ureter; KX, ureteric pore; MA, mantle lobe; MC, mantle collar; MG, mantle gland; P, penis; PP, penial pilaster; PPM, main penial pilaster; PPS, pocket stimulator; PRM, penial retractor muscle; PV, penial verge; S, spermatheca; SS, spermathecal stalk; UT, uterus; UV, free oviduct; V, vagina; VD, vas deferens; X, carrefour; Z, digestive gland.

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# Population characteristics of the gastropod *Cantharidus pulcherrimus* on intertidal platforms in the Perth area of Western Australia

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## ABSTRACT

The trochid gastropod *Cantharidus pulcherrimus* is shown to be abundant on intertidal rock platforms in the Perth metropolitan area of Western Australia, where it is concentrated in the *Sargassum* algal zone. In this zone *C. pulcherrimus* is found living on macroalgae rather than the underlying rock. Density of snails varies seasonally, with maximum density occurring in summer and minimum density in autumn. Recruitment of juveniles into the population occurs during the winter (June-August). The young snails grow rapidly and spawn at one year of age in March or April. A small proportion of the adults survives for a second year. Loss of snails as macroalgae are washed from the platform by winter storms is the largest known source of mortality. The life history strategy of *C. pulcherrimus* is discussed in relation to that of other trochids.

## INTRODUCTION

The shoreline along the Perth metropolitan area of the central west coast of Western Australia is dominated by extensive sand beaches interrupted by small beachrock platforms. The platforms vary in tidal height, but most are at an intertidal level of about 0.4m in an area where the maximum tide range is about 1m. The geology of the platforms was described by Fairbridge (1950) and Semeniuk and Johnson (1985). The latter authors distinguished four types of platforms depending on the inshore structure of the platform and sandy beach. While the inshore structures vary in their characteristics the platforms themselves are more uniform. They are usually flat, often with a seaward rim which traps water on the platform surface at low tide. Solution pipes, channels and

crevices make the surface irregular. The platforms generally extend from a landward cliff, which may have a sandy beach at its base, seaward for distances of a few to 100m. At the seaward margin the platform drops off sharply into a subtidal cliff which extends to the bottom, usually sand, in a few metres of water. The platforms are thus discrete habitats.

The central west coast of Western Australia is a faunal overlap zone with a mixture of three faunal elements: tropical Indo-West Pacific species extending down from the north coast; southern Australian temperate species ranging up from the south coast; and a small (< 10%) group of species endemic to Western Australia (Wilson and Gillett, 1971; Wells, 1980). Platforms along the western end of Rottnest I., 20km offshore from Perth, have a substantial proportion of tropical species. Tropical species are less numerous on platforms along the metropolitan coastline. Those which occur are generally uncommon and contribute little to the total density and biomass of molluscs; molluscs of the metropolitan platforms are virtually all temperate species (Wells, 1985).

In the mid 1960s a commercial fishery was started along the central west coast of Western Australia for the abalone *Haliotis roei* Gray, 1827. A substantial portion of the catch comes from metropolitan platforms. Initially the fishery was divided into discrete commercial and amateur segments. Professional fishermen were permitted to fish only on the subtidal cliffs. While amateurs could also fish in this area most chose to collect abalone on the intertidal platform surface. As abalone populations declined on the platform surface in the early 1980s amateur fishermen began actively fishing on the subtidal cliffs, affecting the commercial fishery. At the same time other species of molluscs, particularly gastropods, were being fished by amateurs but little was known of the extent of the fishing or the species involved. A three year program was initiated in late 1982 with the objective of developing information on platform molluscs, particularly abalone (Wells and Keesing, in prep a; in prep b), for use by fisheries managers. Because of the possibility of using seasonal closures of the platforms as a management technique several studies of the reproductive seasonality and/or seasonal changes in the population structure of platform species were begun.

Trochid gastropods are diverse on the platforms, with nine species having been recorded, several of which reach high population densities. Little is known of the reproductive strategies of Australian trochids except for the work of Moorhouse (1932) and Underwood (1974). *Cantharidus pulcherrimus* (Wood, 1828), a temperate species, was selected for examination because it is the dominant gastropod in some areas of the platforms, reaching a maximum density of almost 500.m<sup>-2</sup>; only mytilid mussels in beds had higher recorded densities. Because of heavy swell conditions during winter, which make the subtidal cliffs inaccessible, the present study was conducted entirely on the platform surface.

## MATERIALS AND METHODS

Three platforms were selected for this study: Waterman, Trigg I. and Cottesloe. Each platform was divided into habitats based on the types of macroalgae present. At Waterman and Trigg I. there were three algal zones: a seaward bare zone largely devoid of macroalgae; an intermediate *Sargassum* zone; and a shoreward inshore platform of mixed macroalgae. The platform at Cottesloe lacks a bare zone but has a broad *Sargassum* zone, the inshore portion of which was sampled in the present study.

To examine horizontal distributions on the platform transects were run across the platform at Trigg I. beginning at the seaward edge of the platform, running through the bare zone and the *Sargassum* zone and into the inshore platform area. Two transects were made on 23 and 25 April 1984 and six months later on 19 and 21 October 1984. There were 10 to 20 stations on each transect spaced at intervals of 2m. At each station the number of *C. pulcherrimus* on *Sargassum*, on other algae and on the platform surface were counted in a quadrat of 50cm x 50cm. The number of *Sargassum* holdfasts was counted and each measured to the nearest 1cm and the percentage of algal cover determined for *Sargassum* and total algae. Algal cover was estimated by using a quadrat 0.25m<sup>2</sup> divided into a grid of 7 x 7 giving 49 intersections. Presence or absence of algae was recorded for each intersection.



To sample annual fluctuations in density of *C. pulcherrimus* samples were conducted in January from 1983 to 1986. A series of eight stations was established in the inshore platform and *Sargassum* zone on each platform. Stations were 5 to 10m apart depending on the extent of the habitat. At each station the number of *C. pulcherrimus* in each of four 0.25m<sup>2</sup> quadrats was counted and density calculated; data were then pooled. The inshore platform on each reef was sampled at quarterly intervals from January 1983 to January 1985 to examine seasonal density variations. The *Sargassum* zone is too rough to be quantitatively sampled in winter and was not studied.

To examine size-frequency characteristics *C. pulcherrimus* were collected at approximately monthly intervals at Trigg I., Waterman and Cottesloe from January 1984 to December 1985. In most months 300 individuals were measured but in some cases fewer snails were available. *Sargassum* was collected from the centre of each platform and placed in labelled calico bags. In the laboratory the *Sargassum* and inside of the bag were washed in freshwater to remove the snails, which were preserved in 10% formalin. Total shell length was measured to the nearest 1mm with calipers.

## RESULTS

A general trend of low density of *C. pulcherrimus* in the bare zone, high densities in the *Sargassum* zone and low densities in the inshore platform at Trigg I. was found in both April and October. *C. pulcherrimus* had mean densities of less than 2.m<sup>-2</sup> in the bare zone (Table 1). The density was nil in the inshore platform in April but 50.m<sup>-2</sup> in October. Mean algal cover on the inshore platform was 0 ± 0% in April, but increased to 56 ± 9% in October. Density was greatest in the *Sargassum* zone both during the April (41.3/m<sup>-2</sup>) and October (170.5/m<sup>-2</sup>) samples. There was not a statistically significant difference between density of *C. pulcherrimus* in the bare zone and inshore platform in either April or October (t-test,  $P > 0.05$ ), but the differences between densities in the *Sargassum* zone and both the inshore platform and bare zones were highly significant in both sampling periods (t-test,  $P < 0.05$ ).

*C. pulcherrimus* is thus clearly concentrated in the *Sargassum* zone. The data collected can be used to determine where the animals occurred in this habitat (Table 2). In both April and October less than 4% of the *C. pulcherrimus* in the *Sargassum* zone were on the bare rock surface; over 96% of the individuals were on algae. In April 91% of the *C. pulcherrimus* were on *Sargassum* but in October only 54% were on *Sargassum* and 43% were on other algae. This suggests that the density of *C. pulcherrimus* in the *Sargassum* zone might be related to either the percent cover of *Sargassum* or of total algae. Table 3 represents the results of linear correlations between density of *C. pulcherrimus* and both percent *Sargassum* cover and percent total algal cover for April and October.  $r$  values ranged from 0.58 to 0.69. There was a statistically significant correlation between density of *C. pulcherrimus* and abundance of both *Sargassum* and total algae in both April and October (t-test,  $P < 0.05$ ) (Table 3).

In addition to the change of the population of *C. pulcherrimus* in the different algal zones there are substantial seasonal and annual variations in the density of the species. Seasonal densities fluctuated considerably (Figure 1). The maximum reached was 134m<sup>-2</sup> at Cottesloe in January 1983. The species was absent on the inshore platform at Waterman in April 1984, when it was completely covered by sand, and there were other occasions when densities were near zero. There is clear evidence of seasonality on all three platforms. In both years the maximum density occurred during January. Numbers declined during the winter to near zero before increasing in spring as recruits entered the population.

Substantial year to year fluctuations in the density of *C. pulcherrimus* were found on all the platforms (Figure 2). The only consistent pattern was that densities were substantially higher in the *Sargassum* zone than on the inshore platform. Annual variations in the two zones of one platform were generally similar, but there were differences between platforms. At Cottesloe densities were high in both zones in 1983, declined to lower levels in 1984, and then stabilized. A similar pattern occurred on the inshore platform at Waterman, but in the *Sargassum* zone density increased by an order of magnitude from 1983 to 1985 before declining in 1986. Density at Trigg I. declined in 1984, rose in 1985 and decreased in 1986.

The size frequency histograms for *C. pulcherrimus* (Figures 3, 4 and 5) show that at the beginning of sampling in January 1984 the population at Cottesloe was unimodal with most of the animals being 6 or 7mm in shell length. At Trigg I. and Waterman the population had greater size variabilities with most animals being 5 to 10mm long. By April 1984 the graphs for all three reefs were clearly unimodal, composed of adult individuals 6–12mm long. A small proportion (2%) of the population at Trigg I. and Waterman consisted of juveniles 2mm long. In June the size frequency histogram for Cottesloe changed substantially with recruitment of juveniles 0–2mm long into the population. These animals constituted 71% of the population in June. By July they were predominately 1–3mm long and the adults had disappeared. The main settlement period at Trigg I. and Waterman started a month later, with a substantial portion of the population on both reefs being small juveniles in July. By August virtually all of the population was young of the year at Trigg I. but some individuals of the 1983 year class survived at Waterman at least until November 1984. The populations of *C. pulcherrimus* at Waterman and Cottesloe continued to grow through the summer months. The population at Trigg I. was bimodal in January 1985, either due to a late settlement in 1984 or a sampling artefact, but graphs for subsequent months were unimodal.

There were a few small individuals in the population at Waterman and Trigg I. in March 1985 but these had disappeared by April. The 1985 recruitment began in June and continued until September. By December the 1985 young had grown to a mean size of 4.4mm. Recruitment at Trigg I. began a month later (July) and at Waterman it commenced in August.

Figures 6, 7 and 8 show the mean size of the various year classes of *C. pulcherrimus* over the two year period of January 1984 to December 1985 on the three platforms. Only means of year classes with more than 25 individuals in a given month are shown. At the beginning of sampling in January 1984 the populations were composed entirely of large individuals spawned in the autumn of 1983. Mean sizes ranged from 6.4mm at Trigg I. to 8.0mm at Waterman. By February the animals had reached nearly their maximum mean size and growth had slowed to near zero. The 1983 year class remained detectable in the populations for varying periods — until June 1984 at Cottesloe and September at Trigg I. At Waterman the 1983 group was still present in February 1985 and had a mean size of 10.5mm. In March 1985 the individuals spawned in 1983 were indistinguishable from the 1984 animals.

The 1984 year class appeared in the populations in June and July. The clearest growth data are from Cottesloe, where juveniles had a mean length of 1.3mm in June 1984 and grew rapidly to 7.1mm in February 1985, then slowed so the animals reached 8.5mm by August. While the data for Trigg I. are not as clear they show a rapid growth of the 1984 class during the spring and summer months with growth tapering off in the autumn as the animals reached adult size and presumably energy was channelled into gamete production. The 1984 year class fluctuated in mean size on the three platforms after about March 1985. The 1985 year class began to be distinguishable in June at Cottesloe, July at Trigg I. and August at Waterman. While the Waterman recruitment was the latest of the three platforms the animals were first detected at a mean size of 3.2mm, suggesting recruitment had actually been earlier. If the lines of growth are extrapolated back to an initial size of 0.0mm an estimate of the spawning season can be obtained. The mean size of the early months of each year class for Waterman fluctuated too much to obtain a reliable estimate. If the Cottesloe and Trigg I. data are used an estimate can be obtained that reproduction must have occurred in March/April.

If the graphs for the three platforms are superimposed it can be seen that the populations of *C. pulcherrimus* on the three platforms share basic features. Reproduction occurs in March/April of each year. Growth of juveniles is rapid through the next year until a mean size of 8 to 10mm is reached in March, when the animals are about a year old. After spawning the adults persist as a declining proportion of the population for several months until late winter. Within this general pattern there are important, consistent differences between Cottesloe and Waterman with Trigg I. being intermediate. The maximum mean size obtained by the 1983 and 1984 year classes at Cottesloe were 8.5mm. Animals at Trigg I. and Waterman were larger, reaching mean sizes of up to 10.0mm. The previous year class disappeared completely at Cottesloe in both 1984 and 1985, but at Waterman in both years some adults remained in the population until they became indistinguishable from the previous year class.



TABLE 1. Comparison of densities of *Cantharidus pulcherrimus* in three habitat zones on the platform at Trigg I.

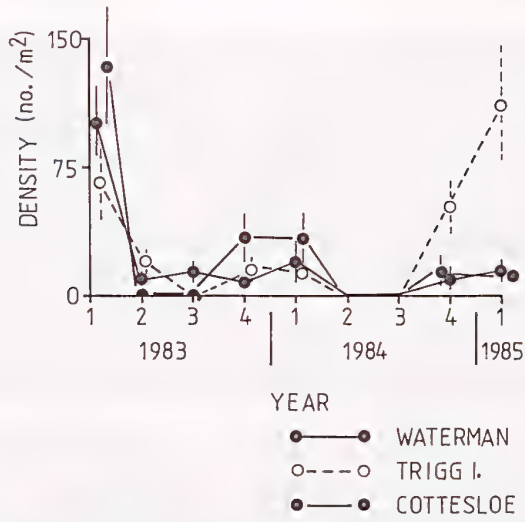
Zone	No. strn.	23-25 April 1984	No. strn.	19-21 October 1984
		Density of <i>C. pulcherrimus</i> (No. m <sup>-2</sup> + 1 S.E.)		Density of <i>C. pulcherrimus</i> (No. m <sup>-2</sup> + 1 S.E.)
Bare zone	5	0.8 + 0.8	5	1.7 + 1.2
<i>Sargassum</i> zone	16	41.3 + 13.6	8	170.5 + 24.5
Inshore platform	4	0 + 0	21	50.5 + 11.9

TABLE 2. Comparison of densities of *Cantharidus pulcherrimus* on *Sargassum*, on other algae and on rock in the *Sargassum* zone of the platform at Trigg I.

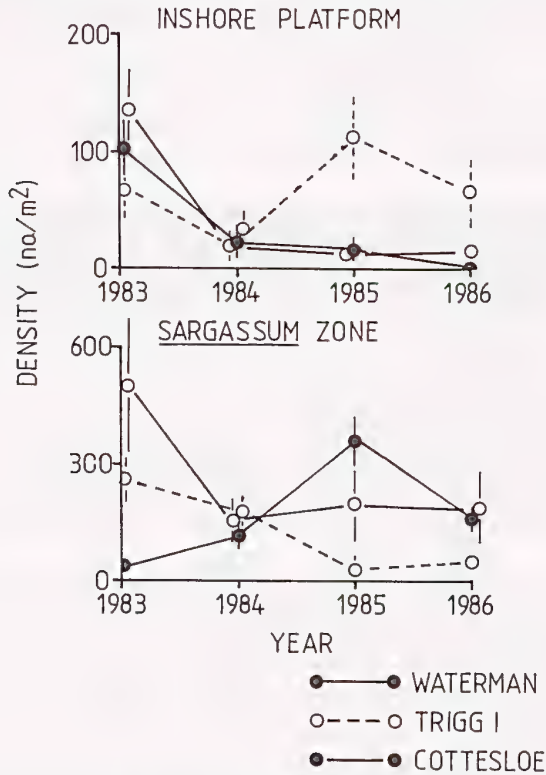
	23-25 April 1984	Algal cover (% ± 1 S.E.)	19-21 October 1984	Algal cover (% ± 1 S.E.)
	Density of <i>C. pulcherrimus</i> (No. m <sup>-2</sup> ± 1 S.E.)		Density of <i>C. pulcherrimus</i> (No. m <sup>-2</sup> ± 1 S.E.)	
On <i>Sargassum</i>	37.8 ± 13.1	31.5 ± 7.2	91.5 ± 18.6	54.4 ± 7.9
On other algae	2.3 ± 1.3	13.1 ± 4.2	73.0 ± 13.9	33.7 ± 6.9
On rock	1.2 ± 0.9		6.0 ± 2.6	
Total	41.3 + 13.6		170.5 + 24.5	

TABLE 3. Linear correlation between density of *Cantharidus pulcherrimus* and percent cover of *Sargassum* and total algae in the *Sargassum* zone on the intertidal platform at Trigg I. in 1984. The correlation is presented in the equation  $Y = a + bX$  where Y is the density of *C. pulcherrimus*, a and b are constants and X is the percent algal cover.

	a	b	r	r <sup>2</sup>	Significance (t-test, 0.05 level)
April					
<i>Sargassum</i>	-0.58	1.29	.6927	.4799	*
Total algae	-7.49	1.09	.5795	.3358	*
October					
<i>Sargassum</i>	58.79	2.05	.6591	.4344	*
Total algae	-370.86	6.06	.6360	.4045	*

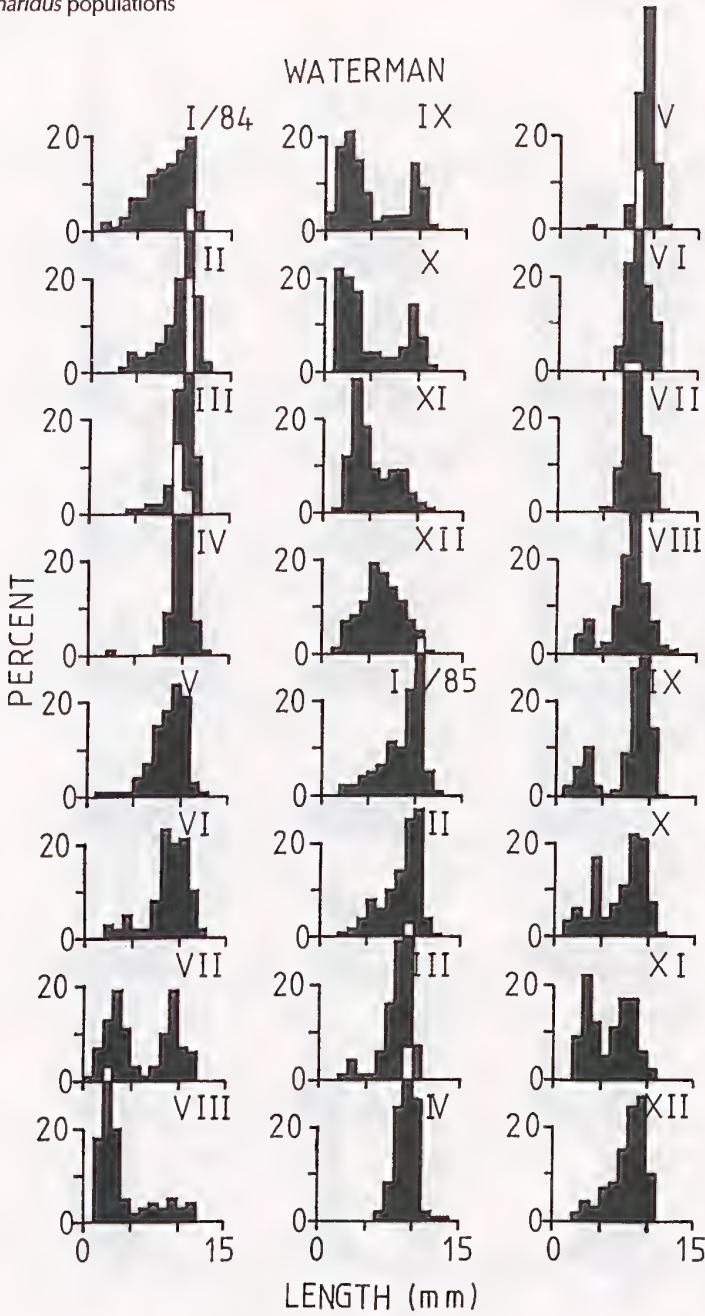


1. Seasonal variations in density of *Cantharidus pulcherrimus* on the inshore platform of three intertidal platforms in the Perth metropolitan area. Means and one standard error are shown.

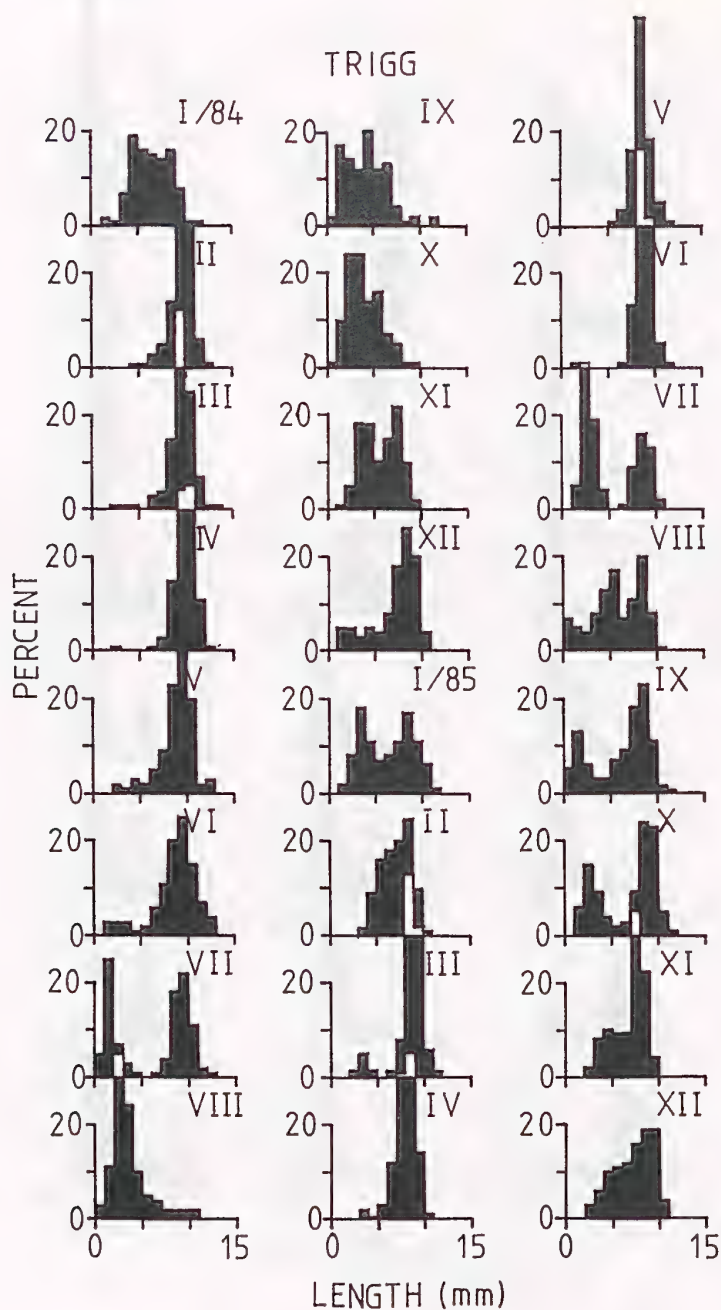


2. Annual variations in summer density of *Cantharidus pulcherrimus* in the Sargassum zone and on the inshore platform of three intertidal platforms in the Perth metropolitan area. Means and one standard error are shown.



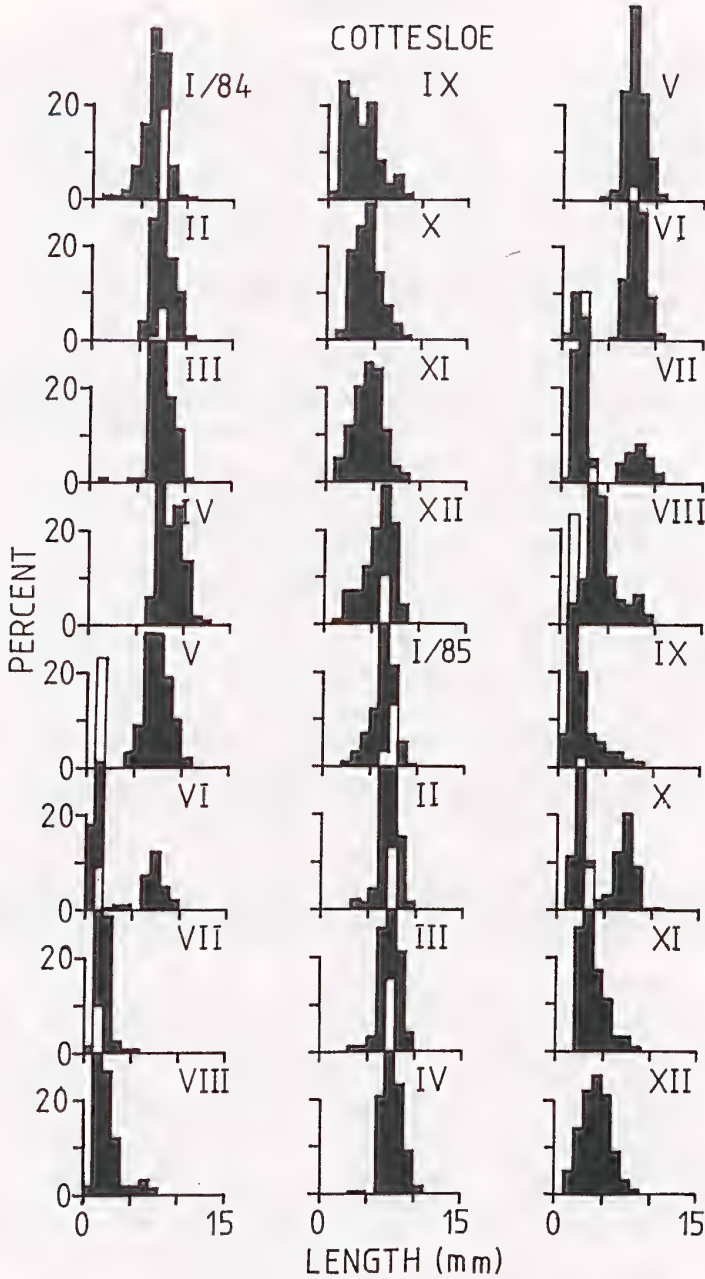


3. Size frequency characteristics of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Waterman at monthly intervals from January 1984 to December 1985.

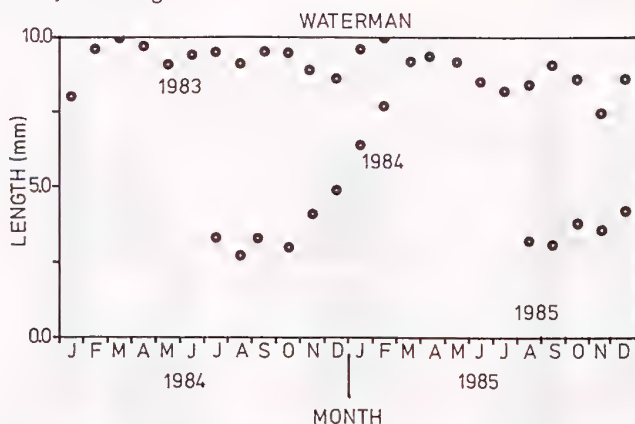


4. Size frequency characteristics of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Trigg I. at monthly intervals from January 1984 to December 1985.

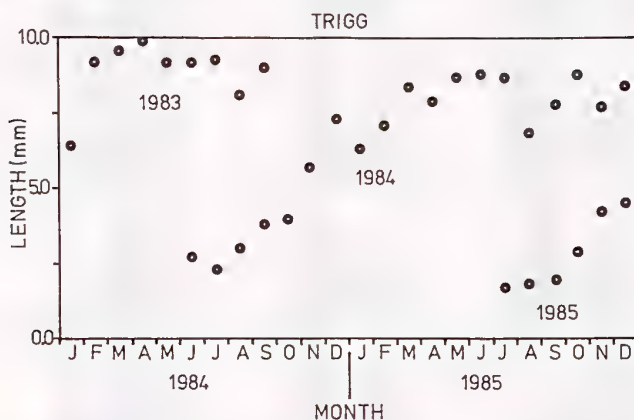




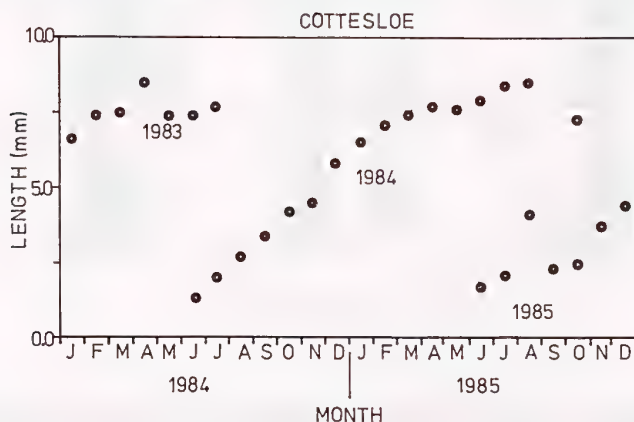
5. Size frequency characteristics of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Cottesloe at monthly intervals from January 1984 to December 1985.



6. Mean size of year groups of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Waterman at monthly intervals from January 1984 to December 1985.



7. Mean size of year groups of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Trigg I. at monthly intervals from January 1984 to December 1985.



8. Mean size of year groups of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Cottesloe at monthly intervals from January 1984 to December 1985.

## DISCUSSION

Most archaeogastropods are dioecious and lack a penis. They are broadcast spawners, males and females both expelling gametes into the surrounding water column where fertilization takes place. After brief planktonic trochophore and veliger stages the young settle to the bottom to begin their juvenile life (Webber, 1977). The family Trochidae has hundreds of species (Abbott and Dance, 1982) but the reproductive strategies of only about a dozen have been studied. Some of the species examined are broadcast spawners with a planktonic veliger stage (Desai, 1966; Paine, 1971; Webber, 1977; Heslinga, 1981; Joska and Branch, 1983) but other species deposit benthic egg masses from which the young hatch as crawling young (Anderson, 1960; Duch, 1969). Even in species which undergo their entire larval development in the water column the planktonic stage is short, on the order of a week or less (Desai, 1966; Heslinga, 1981; Joska and Branch, 1983). The reproductive strategy of *C. pulcherrimus* was not studied. If the species has a veliger stage, as many of the previously studied trochids do, it would allow the repopulation of platforms by veligers spawned on adjacent platforms. Both young and adult *C. pulcherrimus* congregate on benthic macroalgae, particularly *Sargassum*. The macroalgae are easily dislodged by waves and swell, providing a second mechanism for dispersal of snails over the relatively short distances from one platform to another.

As with the reproductive strategy, reproductive periodicity has been studied for few species of trochids. Most of the temperate species examined have a single discrete spawning season which may last for several months (Paine, 1971; Underwood, 1972). *Oxystele variegata* (Anton, 1838) in South Africa has two distinct spawning seasons, February and September/October (Joska and Branch, 1983). While many tropical molluscs spawn year round the tropical trochids studied, *Tegula excavata* (Lamarck, 1822) in Barbados (Lewis, 1960) and *Euchelus gemmatus* (Gould, 1841) in Hawaii (Duch, 1969), both have restricted breeding seasons. The temperate species *Austrocochlea constricta* (Lamarck, 1822) studied in Sydney (Underwood, 1974) and the subantarctic *Cantharidus coruscans* (Hedley) (Simpson, 1977) are the only trochids known to spawn throughout the year. *C. pulcherrimus*, with a discrete spawning period in March/April thus fits into the general trochid pattern. Variation in the spawning periodicity of *Monodonta lineata* (Da Costa, 1778) in England has been found at different localities and in different years (Desai, 1966), paralleling the differences found between different platforms (particularly Cottesloe and Waterman) and between 1984 and 1985 for *C. pulcherrimus*. The extreme case reported was the failure of *Gibbula cineraria* (Linnaeus, 1758) to spawn in 1970 at Plymouth, England (Underwood, 1972). Such reproductive failure did not occur in *C. pulcherrimus* during the study period.

There are few data available on the lifespans of trochids. McQuaid (1982) showed that *O. variegata* in South Africa reaches a size of 14mm in one year, 18mm in two, and a proportion of the population was thought to survive beyond two years. *Tegula funebris* (A. Adams, 1855) in Washington live up to 32 years (Paine, 1971).

Causes of mortality have not been directly investigated in *C. pulcherrimus*, but several can be discussed. Tides in the Perth area are small, with a maximum range of 1m, but there is a seasonal variation in sea level of about 0.3m (Hodgkin and Di Lollo, 1958). During winter the prevailing southwesterly or southerly airflow tends to be onshore and increases sea level. In summer the prevailing winds are offshore, decreasing tidal levels. Summer is also the season when easterly airflow generated by atmospheric high pressure systems may persist for several days, tending to keep water off the platforms. Air temperatures are high, up to 40°C or more, resulting in massive mortalities on the platforms (Hodgkin, 1959). Substantial decreases in the density of *C. pulcherrimus* possibly from high temperatures were recorded between January and April in both 1984 and 1985. However, *C. pulcherrimus* survived a bout of high temperatures in October 1985 when massive mortalities occurred amongst other molluscs (pers. obs.).

A second potential cause of mortality is the postreproductive death of adults. Such mortality has been suggested for *Nodilittorina unifasciata* (Gray, 1827) on the cliffs shoreward of the platforms at Waterman. *N. unifasciata* suffered substantial mortality during summer. As the summer conditions took the highest toll of adults it was considered to be postreproductive mortality (Wells, 1984). Declines in the population of *C. pulcherrimus* on the platform occurred between January and April, before the spawning season of *C. pulcherrimus*, suggesting that the cause was not



postreproductive deaths of adult individuals.

Macroalgae on the platforms are seasonal, growing rapidly and being most diverse in summer. The macroalga *Ecklonia radiata* occurs on the platforms, particularly Cottesloe, but has been studied in subtidal locations. The greatest loss of *E. radiata* is during the heavy swell conditions of the winter months (Kirkman, 1981). *Sargassum* and other macroalgal populations on the platforms are substantially reduced by autumn and winter storms and thrown upon the beach in extensive drift beds (Lenanton, Robertson and Hansen, 1982). As the macroalgae are torn off the platforms most of the attached snails will be washed upon the beach and die, a major source of mortality for *C. pulcherrimus* since it lives on macroalgae rather than the underlying rock.

## ACKNOWLEDGEMENTS

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## Reproduction and development of *Onchidium damelii* Semper, 1882

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No information on reproduction or embryonic development of *Onchidium damelii* Semper, 1882 has been located.

Field observations were made at Magnetic Island (19°11'S, 146°50'E) off the east coast of Australia on 34 occasions (daylight low tides) from February to December (1981). On these occasions animals were observed for evidence of copulation and areas where known onchiid populations existed were searched for egg masses.

Mating was observed from September to June. No environmental influences on copulation were noted and mating occurred at any time during the daylight low tide emergence period. No particular behavioural pattern was observed and mating appeared to be a result of chance meetings.

The non-breeding period (July, August) coincides with the coolest time of the year when sea temperatures are approximately 20 to 22°C in the Townsville area (Kenny, 1974).

Fretter (1943) recorded egg capsules for only a two to three month period in summer for *Onchidella celtica* in Britain and Stringer (1969) noted relatively short (two to three month) breeding seasons for three species (*Onchidella flavescentis*, *O. campbelli* and *O. nigricans*) in New Zealand. Of these *O. flavescentis* breeds in winter-spring (August to October) while the other two species are summer breeding forms (Stringer, 1969). A reproductive period of three to four months has been reported for *Onchidium verruculatum* but the timing appears to vary in different parts of the geographic range of the species, being listed as June to October in Kuwait (McFarlane, 1979) and December to March on the west coast of India (Deshpande *et al.*, 1980).

The present observations recorded only single pair copulation as was reported for *Onchidella celtica* by Fretter (1943), but Stringer (1963) noted that for *Onchidella nigricans* copulation may involve several individuals in the form of a ring and McFarlane (1979) observed copulatory chains of *Onchidium verruculatum*.

The recipient individuals from pairs observed mating were collected and maintained in the laboratory in high humidity on a seawater soaked substrate at 23°C until eggs were laid. Animals brought into the laboratory after observed mating laid eggs 17 to 19 days after copulation.

Egg masses, in the field, were found only attached in cavities in the buttress roots of the mangrove *Ceriops tagal*. They were approximately 6x4x0.5cms in size and of irregular ovoid shape. Random counts gave estimates of 100 to 200 thousand eggs per egg mass.

The large number of eggs recorded from egg masses of *Onchidium damelii* contrasts with the relatively small numbers noted for some other species — *Onchidella celtica*, 60 to 100 (Fretter, 1943); *O. flavescens*, 22 to 90 and *O. campbelli*, 28 to 120 (Stringer, 1969). Stringer (1969) observed much larger egg numbers — 500 to 11,000 — from egg masses of *O. nigricans*.

Awati and Karandikar (1948) reported the eggs of *Onchidium verruculatum* arranged in a single longitudinal row; the present observations showed an irregular arrangement of eggs in several rows for *O. damelii* egg masses.

The individual eggs of *Onchidium damelii* were spindle shaped with spike-like processes projecting from the ends of the spindle.

Egg dimensions were length, mean 0.193mm  $\pm$  0.057 (S.D.) (excluding terminal projections), diameter, mean 0.123mm  $\pm$  0.029 (S.D.); n = 26 from three egg masses.

Comments in the literature on onchidian development have not included egg sizes for other species (Fretter, 1943; Stringer, 1963, 1969).

*Onchidium* egg masses recovered in the field were cultured in aerated seawater (35‰) at 23°C. Eggs were removed daily and after live observation with a dissecting zoom microscope were preserved in 10% formol calcium acetate. The developmental stages of the embryos and the veliger larvae were photographed with a Zeiss photomicroscope using the Nomarski differential interference contrast method.

The embryonic stages of *O. damelii* show typical molluscan development with a spiral cleavage pattern. Development from the single cell stage to the multicell (early blastula) stage occurred within six hours from the time of laying.

The earliest veliger stage was observed on day 4 rotating within the egg capsule by means of velar cilia. The veligers undergo considerable development prior to emerging as free-swimming larvae, which were first observed on day 12. They have the appearance of characteristic gastropod veligers, with thin transparent shell, ciliated bilobed velum, small foot bearing on operculum, pair of statocysts, complete digestive tract, and well developed retractor muscle.

Live veliger larvae showed considerable variation in overall dimensions and in relative size of the velar organ. Larval length varied from 0.15mm to 0.26mm (n = 9). Fretter (1943) recorded 0.3mm as "overall length" of the veliger larva of *Onchidella celtica* and Stringer (1969) lists the "size" of veligers of *O. nigricans* as 0.21mm, *O. flavescens* 0.27mm and *O. campbelli* 0.30mm.

Veliger shell maximum diameter measurements varied from 0.14 to 0.19mm (n = 7) for *O. damelii*. Shell measurements have not been found in the literature for other species.

In the laboratory the pelagic stage lasted between seven and ten days before death occurred. Little change in the size or organization of the veligers was noticed during this phase.

Settlement or metamorphosis was not observed.

The timing of development of *Onchidium damelii* — veliger larva formed on day four, released on day 12 and free swimming for more than seven days is comparable to that given for *O. verruculatum* — veliger formed on day five, released on day 15 and free swimming for

approximately five days prior to metamorphosis (Awati and Karandikar, 1948). Stringer (1963) states the veliger of *Onchidella nigricans* is released after 25 days of development (a longer period than for *Onchidium damelii*) and is planktonic for seven days (similar to *O. damelii*).

The aquarium temperature (23°C) was near the lower limit of the recorded field temperatures and it is possible that development of *O. damelii* may be more rapid in nature.

Three species of *Onchidella*, *O. celtica*, *O. flavescens* and *O. campbelli* have been described as having direct development without a free swimming veliger phase (Fretter, 1943; Stringer, 1963). Awati and Karandikar (1948) and Stringer (1963) have described free veliger stages, from *Onchidium verruculatum* and *Onchidella nigricans* respectively.

The three species with direct development — *Onchidella celtica* (Fretter, 1943), *O. flavescens* and *O. campbelli* (Stringer, 1969) — are those with relatively small numbers of eggs in the egg masses, while two species with free swimming veligers *O. nigricans* (Stringer, 1969) and *Onchidium damelii* have large egg numbers.

Stringer (1963) related the presence of a free larval stage to the marine habitat of species; and commented that the restriction of *O. damelii* to mangrove-estuarine locations was "a link in the invasion of land". In contrast it has been suggested that *O. damelii* has reinvaded the marine habitat from the terrestrial environment (Arey and Crozier, 1921; Starobogotov, 1976; Climo, 1980). The current observations of a free swimming veliger stage in the developmental sequence of *O. damelii* support the suggestion of a distinct marine association.

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## BOOK REVIEW

Nudibranchs of Southern Africa. A Guide to Opisthobranch Molluscs of Southern Africa. By Terrence Gosliner. 1987. Sea Challengers, 4 Somerset Rise, Skyline Forest, Monterey, CA 93940 USA. 136 pages, 268 colour plates. \$ (US) 34.95, paperback.

This book has been eagerly awaited for several years by all malacologists interested in opisthobranchs. The book has been well worth the wait. It begins with introductory pages describing the basic features of the biology of opisthobranchs: their evolutionary history, defense mechanisms, feeding, reproduction, systematics, and biogeography. This section also includes notes on how to collect opisthobranchs. The second section is a taxonomic listing of the species known from southern Africa followed by a key to the species included in the book. The key is accompanied by a glossary of terms and excellent black and white illustrations of various features of the animals.

The bulk of the book is the section describing 268 of the species which are currently known to occur in southern Africa. The photos are not comprehensive as a number of species reported to occur in the area are not included and no doubt further collecting will reveal the presence of many more. For each species the family is given, followed by scientific name, notes on taxonomy, natural history, occurrence and distribution, and a colour photograph. The inclusion of a colour photograph is essential for these animals, which so often lose most of their colour in preservative, and the photos are in general outstanding. These are the real strengths of the book.

Opisthobranch taxonomy is difficult and the identification of many of even the most common species in most parts of the world is uncertain. Of the 268 species illustrated in the book, 100 are considered to be undescribed. Dr. Gosliner is an acknowledged opisthobranch expert and the identifications are as sound as are available with our current knowledge of the group. No doubt various experts will disagree about the classification of many of the species. The cover photo for example is of a species listed as *Nembrotha purpureolineata* which was described by C.H. O'Donoghue from the Houtman Abrolhos, Western Australia. The illustrated specimen differs considerably in colouration from specimens from the Abrolhos, and probably is a different species.

There are unfortunately several drawbacks to the layout of the book which detract the ease which it can be used. The localities in which species have been found are recorded in the text but the map showing where the localities are is hidden on the next to the last page. Sizes of the photographed specimens are listed on the back page. Size information would have been more easily used if it was included with the species description, allowing ready size comparisons of species of the same family shown on consecutive photographs. Features of the opisthobranch orders are summarised in the systematics section in the beginning of the book. Species in the text are arranged in systematic order but there is no description anywhere of the basic features of a family.

These criticisms are not meant to indicate a negative attitude towards the book. In general it is well presented and the printing is good. The book is an excellent contribution to our knowledge of opisthobranchs. As many of the species included occur widely over the Indo-West Pacific, the book is of interest to readers over a much wider geographical range than the title implies. I recommend the book for anyone interested in molluscs, and believe it will be essential for the personal library of every opisthobranch worker.

F.E. Wells

## Observations on Australian Solemyidae

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### ABSTRACT

Two species of Australian Solemyidae are examined. Gross structure, the condition of the gut, the histological organization of the gills, and the presence of intracellular gill bacteria are noted. *Solemya velesiana* (Iredale) is a small, intertidal protobranch with large ctenidia, and a functional gut. The species oxidizes sulphide and intracellular gill symbionts appear to contribute to its economy. Museum specimens of a species assigned to *Solemya australis* Lamarck also have large ctenidia with intracellular bacteria. The gut of this species is much reduced and the organism thus must be more dependent on sulphide-oxidizing symbiosis.

### INTRODUCTION

For more than a century the living Solemyidae have been objects of curiosity because of their much reduced alimentary tracts, a condition first noted by Pelseneer in 1891. The species discussed by Yonge (1939), *Solemya velum*, and *S. togata*, are small deposit feeders, and their gut reduction roused no suspicions. However, Owen (1961) pointed out that in the relatively large New Zealand species, *S. parkinsoni*, the minute gut could not possibly provide an adequate digestive process and he suggested that extra-organismic digestion might occur in the mantle cavity. A more striking problem was raised by the discovery of a gutless species *S. reidi* (Reid and Bernard, 1980). Coincidentally, the gutless Pogonophora of the Galapagos Rift hydrothermal vent communities were discovered to possess symbiotic bacteria that could use the energy of sulphide oxidation to fix carbon dioxide, and similar symbionts were then discovered in the ctenidia of *S. reidi* and *S. velum* (Cavanaugh et al., 1981; Felbeck et al., 1981; Felbeck, 1983; Cavanaugh, 1983). It may be inferred that other gutless Solemyidae such as *S. borealis* and *S. solen*, as well as gutless members of the solemyoid family Nucinelidae, are largely dependent on the sulphide-oxidizing symbiosis, although the uptake of dissolved organic molecules is a potential nutrient supplement in environments where there is much organic debris (Reid, 1987; Shepard, 1986). The symbiosis has also been discovered in Solemyidae that retain the gut, and two questions therefore arise: to what extent does normal alimentation satisfy the nutritional requirements of such species, and how universal is the occurrence of the symbiosis in the Solemyidae? Reid and Brand (1986) argue that the sulphide-oxidizing symbiosis was the major driving force of the evolution of the solemyoid Protobranchia, and although this argument would not be greatly vitiated by the discovery of a

species that lacked the symbiosis, more comprehensive evidence on the symbiosis and its morphological correlations is desirable. For this purpose we examine here two species of Australian Solemyidae that possess alimentary tracts.

## MATERIAL AND METHODS

Specimens of *Solemya velesiana* (Iredale) were collected at Pioneer Bay, Orpheus Island, Queensland, in the mid-tidal area of the mud flats behind the fringing reef. Some were examined by dissecting microscope at the laboratory of James Cook University on Orpheus Island. Particles of alumina, carborundum, latex and sephadex (in the size range of 10  $\mu\text{m}$ -120  $\mu\text{m}$ ) were used to detect ciliary movement of particles. The particles found in natural pseudofaeces were also measured. Others were fixed in Bouin's fixative for subsequent embedding in JB4 plastic. Some specimens were fixed in glutaraldehyde for embedding in epon for transmission electron microscopy, and some glutaraldehyde-fixed material was dried and gold coated for scanning electron microscopy. Details concerning fixation and staining are provided by Reid and Brand (1986). A large specimen of *Solemya australis* Lamarck from King George Sound was examined for the morphology of the mantle cavity, and partially dissected to study the gut. Other specimens that had been collected intertidally in sand near Perth, Western Australia and had been fixed in formalin, and preserved in alcohol, were embedded in JB4 polymethacrylate for serial sectioning, or epon-embedded and sectioned for transmission electron microscopy. One specimen was studied by scanning electron microscopy.

Serial sections of specimens of *S. velesiana* and *S. cf. australis* (see below) were stained with periodic acid Schiff stain (PAS), which indicates the presence of polysaccharides, and also stains the symbiotic bacteria. Alcian blue was used to detect acid mucopolysaccharide, with eosin as the counterstain. Control sections treated with diastase ( $\alpha$ -amylase) provided information on the distribution of glycogen.

### Note on the taxonomy of *Solemya* in Western Australia

At the present time only *Solemya australis* is recorded from the southern part of Western Australia (Cotton, 1961; Roberts and Wells, 1980). There is, however a possibility that as many as three species may have been identified as *S. australis*. Slack-Smith (pers. comm.) has raised a question concerning the identity of the most commonly collected intertidal *Solemya* which always appears to be in the less than 1cm size range of *S. velesiana* and *S. terraereginae* (Iredale), the latter being a tropical species that we did not obtain. Among the larger individuals held by the Western Australian Museum we noted some variability in shell shape and in the relative sizes of the gills; but we do not possess sufficient material to clarify this issue. We have opted for the conservative tactic of describing three individuals, of intermediate sizes, which were all consistent in relative gill size, labial palp form, gut size, and in having an anteriorly expanded shell, and of calling these *Solemya cf. australis*, noting here that this will probably be subject to subsequent taxonomic revision. A specimen of this type has been lodged with the Western Australian Museum.

## RESULTS

### Distribution

*Solemya velesiana* occurs intertidally; its type locality being Green Island, Queensland. The bivalve inhabits well-defined, V-shaped burrows that are lined with a thin layer of mucus. The burrows are easily detected while digging since they are marked with an orange-brown halo of ferrous iron which is probably due to the oxidation of iron sulphide in the reducing environment when exposed to the oxygen drawn through the burrows by ventilation currents (Dando et al, 1985). The average depth of the burrows is 15cm and the animals were most commonly found at depths between 5 and 10cm, with the anterior ends uppermost. The sediment below 5cm does not have a strong sulphide odour, and by the Dando olfactory test appeared to have a sulphide content of no more than 0.1  $\mu\text{m}$ , i.e. barely detectable to a human nose of average chemosensitivity (Dando et al, 1985). Depletion of sediment-bound sulphide may require frequent re-burrowing. The species was not found in the high sulphide environment of the upper intertidal mangrove,



nor in cleaner sand in the mid-tidal of other parts of Pioneer Bay. Specimens that had been recently dug up and placed in clean sea water were observed to swim by jetting water through the exhalant opening, in the manner of *S. velum* and *S. reidi* (Reid, 1980).

*Solemya australis* Lamarck, the type species of *Solemya*, is widely distributed in southern Australia (Cotton, 1961). Its preferred environment is not known. Since it is known to be an active swimmer (like other Solemyidae), this species may choose favourable environments. *S. australis* is found in the benthos of its type locality in King George Sound and in the adjacent, shallow Oyster Harbour in the Albany area of Western Australia (Roberts and Wells, 1980). Specimens of *Solemya* cf. *australis* in the collection of the Western Australian Museum have been found intertidally in sand in W. Australia.

### Pallial Functional Morphology

*Solemya velesiana* has large aspidobranchiate, or bipectinate ctenidia, characteristic of the Solemyidae. (Fig 1A, 2A). They are dark brown in colour, which may be due to the presence of haemoglobin and bacteria (Felbeck, 1983; Doeller and Colacino, 1987). The frontal cilia of the distal margins of the lamellae beat ventrally, and particles ranging in size from 10 to 300  $\mu\text{m}$  accumulate to form mucus-bound pseudofaeces which are voided through the exhalant opening. The mucus appears to be produced largely by the hypobranchial gland in the suprabranchial chamber. There is no evidence of particle-sorting by the gills nor any indication of the anterior movement of particles recorded by Yonge (1939) for *S. togata*. The cilia of the gills therefore appear to have only a cleansing function. The labial palps are relatively large, with a basal expansion. As in other Solemyidae there are no sorting ridges and grooves, and the palps may be the homologues of the palp proboscides of the nuculoid Protobranchia (Yonge, 1939). There is no evidence in either of the species under investigation of the separate palp pouch homologues that occur in *S. reidi* (Reid, 1980). In section the palps are crescentic, and the convex and concave surfaces are ciliated. The cilia of the outer convex surfaces beat towards the palp margins, and those of the concave inner surfaces beat towards the base of the palps, whence a narrow ciliated tract carries particles to the mouth. The palps can be extended anteriorly through the pedal gape, but we were unable to observe the natural feeding posture as it might occur in the animal's burrow.

The ctenidia of *Solemya* cf. *australis* are also relatively large but the labial palps are small when compared to those of *S. velesiana* (Fig. 1B and 2B). A distinct food groove runs from the base of each palp towards the mouth.

### Histology and Ultrastructure of Ctenidia

The gill lamellae in the two species under investigation have the same structure as has been reported for *S. reidi* (Reid 1980; Powell and Somero, 1985). The crescentic lamellae are attached by a short septum to the visceral mass (Fig. 3). Each lamella has a double supporting rod of chitin near the ventral margin (Fig. 3 and 4A). The cells distal to the chitinous rod are ciliated and possess numerous mitochondria. Proximal to the chitinous rod is a large blood vessel which communicates with the extensive blood spaces between the two epithelial layers of the lamellae. The proximal lamellar tissue consists of two cell types. The narrow intercalary cells contain mitochondria, and have microvillar distal borders that partially overlap the surfaces of the adjacent bacteriocytes (Fig. 4B). The bacteriocytes, which alternate with the intercalary cells, contain numerous bacteria (Fig. 4B). The bacteria stain strongly with PAS and this staining persists in diastase-treated sections which have lost their glycogen granules. This staining therefore gives a preliminary indication of the presence of bacteria, both in freshly fixed tissue and in museum material. At the EM level the presence of the bacteria can be confirmed e.g. in *S. velesiana* (Fig. 4B) and in museum specimens of *S. cf. australis* (Fig. 4C). High magnification of the museum material confirms that the granular residue of the bacteriocytes does consist of bacteria, with characteristic cells walls and chromosomal content, although the cell membranes of the bacteriocytes have largely disintegrated, and mitochondria are no longer recognisable. In the preparations from this species, the alternating arrangement of bacteriocytes and intercalary cells can be vaguely discerned. Note that the nuclei of the intercalary cells are usually evident, but that because of the large size of the bacteriocytes a given section will miss some of their nuclei (Fig. 4B).

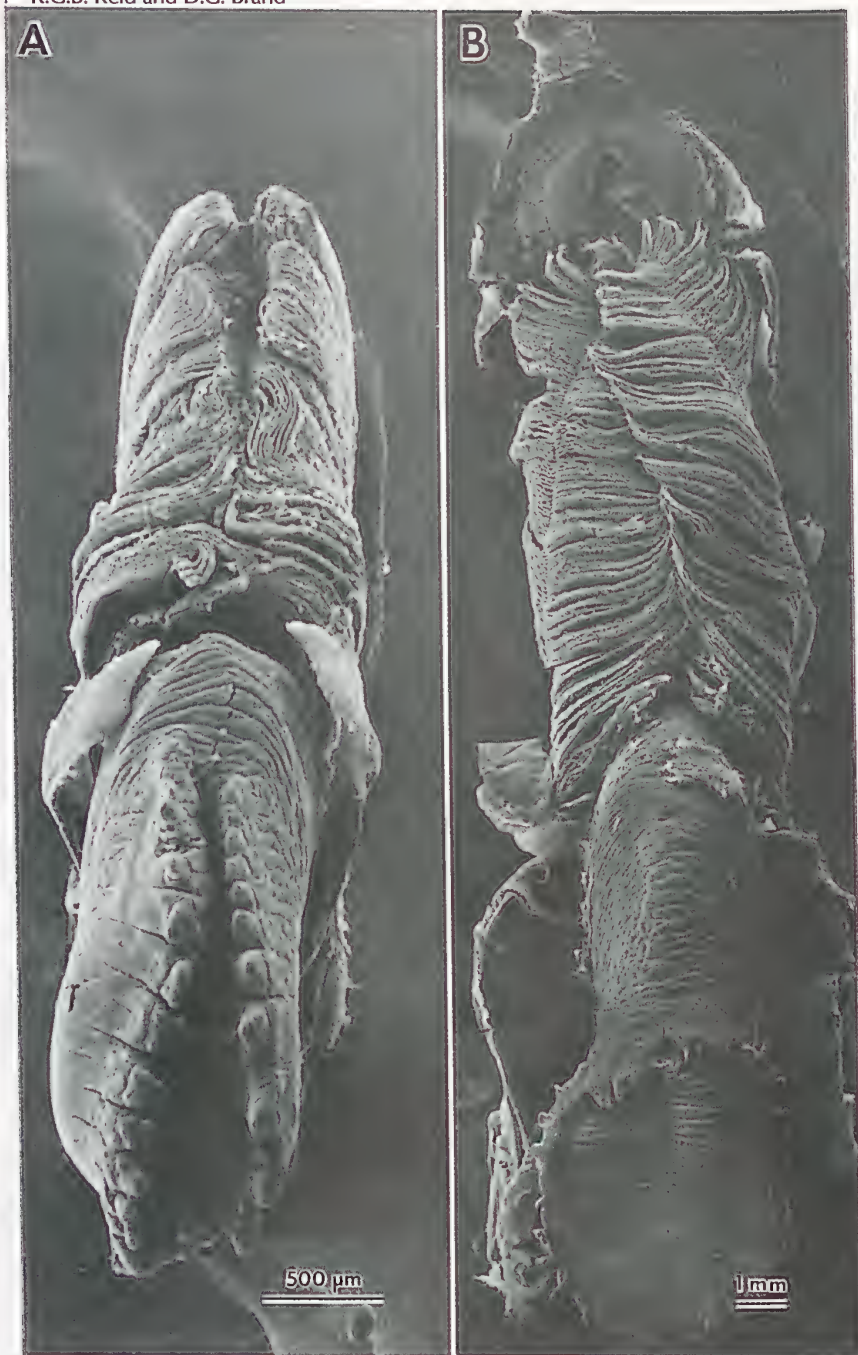


Figure 1.

- A. Scanning electron micrograph of ventral surfaces of *Solemya velesiana*. Shell is removed; foot is anterior.
- B. Composite scanning electron micrograph of ventral surfaces *Solemya* cf. *australis*. Shell is removed; foot is anterior.

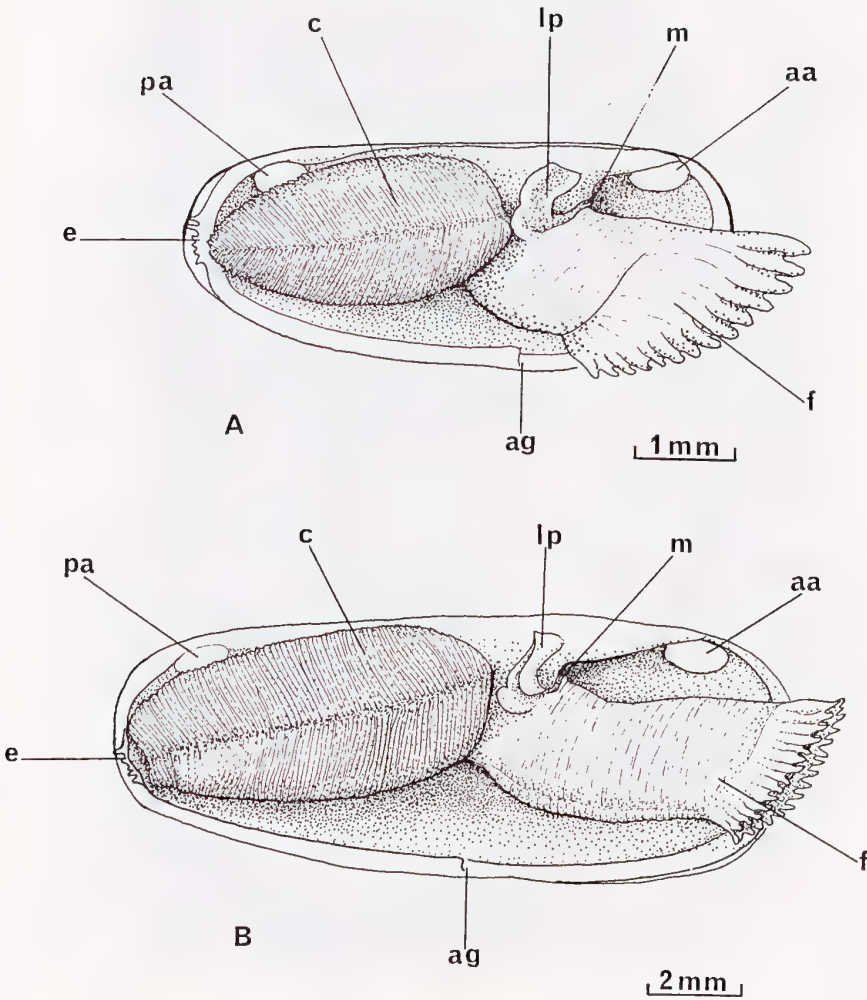


Figure 2.

A. Diagram of right side of *Solemya velesiana*; shell removed.

B. Diagram of right side of *Solemya cf. australis*; shell removed.

Abbreviations: aa — anterior adductor muscle; ag — posterior limit of anterior gape; c — ctenidium; e — exhalant siphon; f — foot; lp — labial palp; m — position of mouth; pa — posterior adductor muscle.



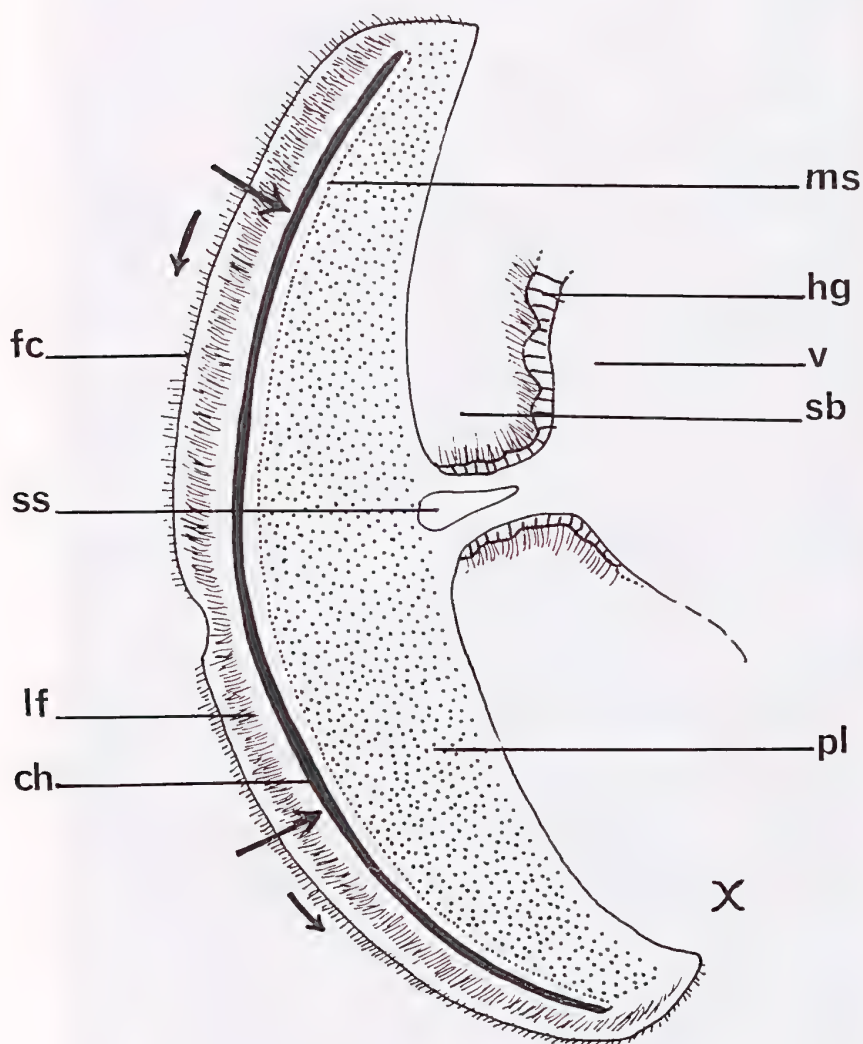


Figure 3.

Stylised diagram of *Solemya* ctenidial lamella. Pseudofaeces collect at X.

Abbreviations: ch — chitinous supporting rod; fc — frontal cilia; hg — hypobranchial gland; lf — latero-frontal cilia; ms — position of marginal blood sinus; pl — proximal region of lamella, made up of bacteriocytes and intercalary cells; s — septum; sb — suprabranchial chamber; ss — septal blood sinus.

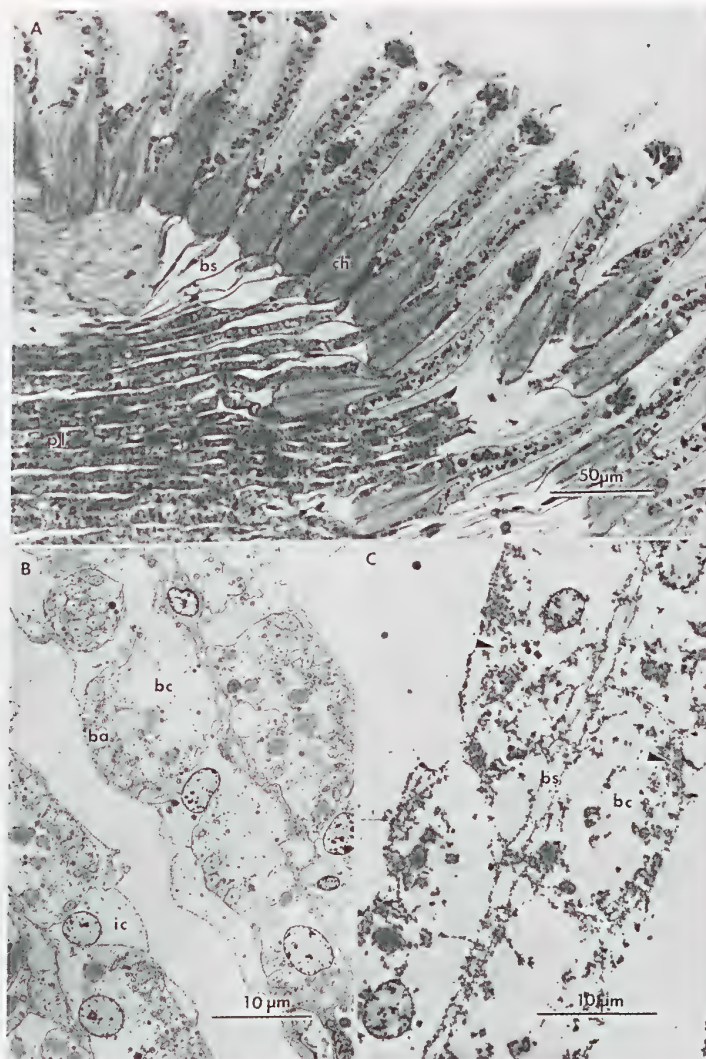


Figure 4.

A. Light micrograph of a transverse section of the gill lamellae of *Solemya velesiana*

B. Transmission electron micrograph of gill lamellae of *Solemya velesiana*

C. Transmission electron micrograph of formalin-fixed, alcohol-stored museum material of *Solemya* cf. *australis*. Arrows indicate bodies that can be determined to be bacteria at higher magnification.

Abbreviations: ba — bacteria; bc — bacteriocyte; bs — blood sinus; ch — chitinous supporting rod; ic — intercalary cell; pl — proximal region of lamella made up of bacteriocytes and intercalary cells.

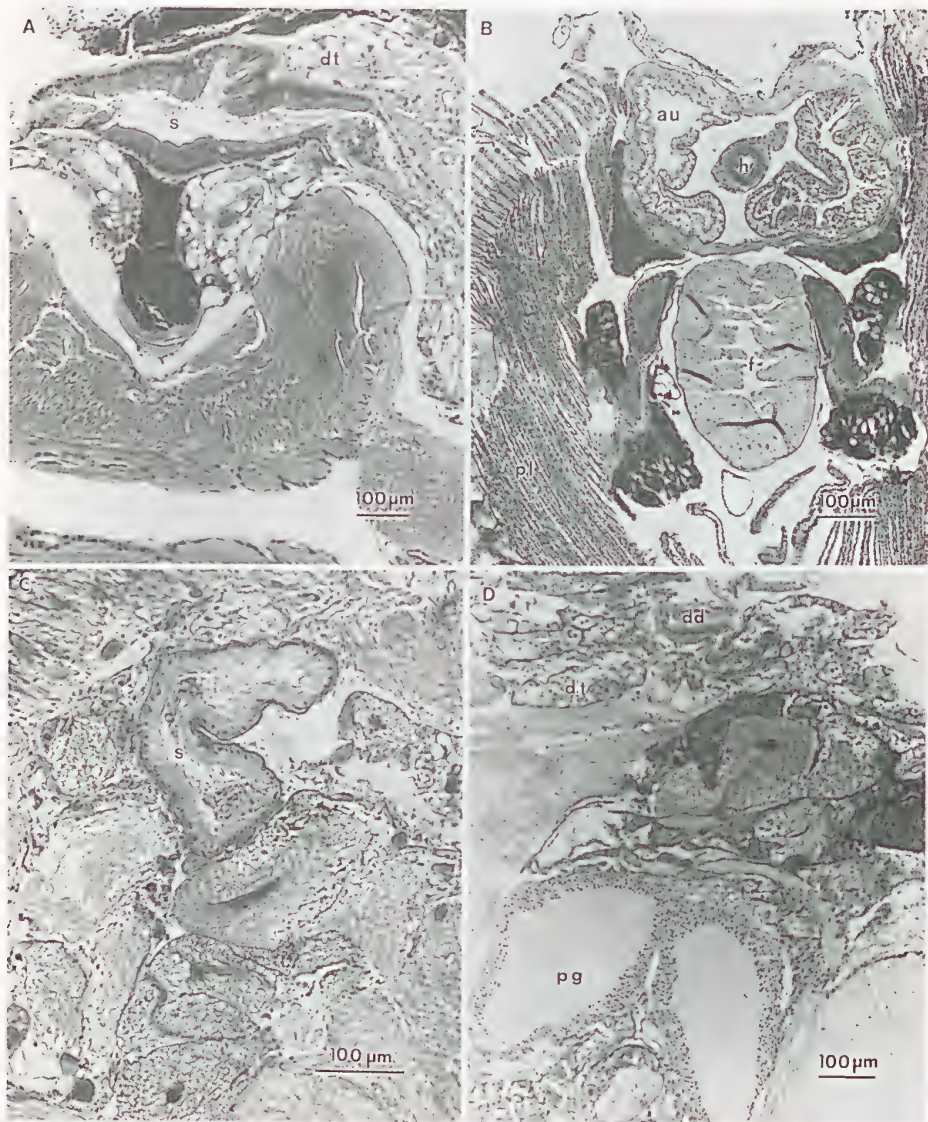


Figure 5.

JB4 (polymethacrylate) transverse sections

A. Gastric region of *Solemya veseliana*

B. Cardiac region of *Solemya veseliana*

C. Gastric region of *S. cf. australis*

D. Region of digestive diverticula and pedal ganglia of *S. cf. australis*

Abbreviations: au — auricle; dd — diverticular duct; dt — digestive tubule; f — foot; h — hind gut; pg — pedal ganglia; pl — proximal region of gill lamellae, containing bacteriocytes and intercalary cells; s — stomach.



### Alimentary Tract

The oesophagus is short in both species. The stomachs differ in relative sizes and complexity. In transverse sections the stomach of a 1cm specimen of *S. velesiana* reaches a maximum of 1mm in diameter (Fig. 5A). The stomach of a 2.5cm specimen of *S. cf. australis* did not exceed 1mm (Fig. 5C). In each species the digestive diverticula consisted of a few small acini (Fig. 5A and D). The diverticular epithelia of *S. velesiana* have large lipid droplets that appear as vacuoles in material that has been dehydrated in alcohol (Fig. 5A). In both species the mid gut is narrow, short and relatively unconvoluted. Particles found in the guts of *S. velesiana* and *S. cf. australis* were in the size range of 5 - 30  $\mu\text{m}$ .

## DISCUSSION

*Solemya velesiana*, and *S. cf. australis* both possess reduced alimentary tracts. This is more common than the gutless condition of *S. reidi*, *S. borealis* and *S. solen* (Reid, 1986). In *S. reidi* there is never a complete, functioning gut; separate rectal, gastric and oesophageal rudiments present in the late pericalymma larvae disintegrate at metamorphosis (Gustafson, 1985). Where present, the gut of most *Solemya* species would not appear adequate to nutritionally support these relatively large, active bivalves. As Owen (1961) remarked concerning the large species *S. parkinsoni* the stomach is barely large enough to contain a single diatom of respectable dimensions. Some indication of the importance of the alimentary tract may be derived from the proportions of the gut and gills relative to the whole organism. On these grounds, the digestive processes of the gut of *S. velesiana* would appear to be a significant source of nutriment. The presence of relatively large labial palps and the lipid depots in the digestive diverticula support this conclusion. Furthermore this species has sources of detrital food from the mangrove and the fringing reefs. The gills are also large in this species, indicating that the sulphide-oxidizing symbiosis is also important.

In *Solemya cf. australis* the gills are relatively large and the gut more reduced than that of *S. velesiana*. Specimens held by the Western Australian Museum are recorded as having been collected intertidally in sand in eelgrass beds. Fisher and Hand (1984) have observed that eelgrass roots may provide symbiotic Lucinidae with a source of photosynthetic oxygen, which along with sulphide is necessary for symbiotic metabolism. Reid and Brand (1986) review the different routes of uptake and internal partitioning of oxygen and sulphide in all bivalves in which the sulphide-oxidizing symbiosis has been found. Powell and Somero (1986) have discovered that in *Solemya reidi* the mitochondria of the host bivalve initiate the sulphide oxidation and produce ATP from the initial oxidation. The role of the symbiotic bacteria would then be the provision of essential amino acids and fatty acids that the bivalves cannot synthesize for themselves. This is also likely to hold in Solemyidae with alimentary tracts which cannot adequately contribute to nutrition. According to our unpublished observations *S. reidi* rapidly absorbs dissolved amino acids and sugars from the environment when these are available. Shepard (1986) has demonstrated that these dissolved organic molecules (DOM) are available at significant levels in environments where organic debris is being decomposed by free-living anaerobic bacteria. This may help to sustain the juveniles of *S. reidi* until the gills and their symbionts have developed adequately.

In those species of *Solemya* that retain guts, the alimentary tract may be particularly important for normal nutrition during the crucial stage between metamorphosis and gill expansion. In the adults the gut may provide an additional route for sulphide absorption (Reid and Brand, 1986).

## ACKNOWLEDGEMENTS

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# Redescriptions of *Cystopelta petterdi* Tate, 1881 and *Cystopelta bicolor* Petterd and Hedley, 1909 (Pulmonata: Cystopeltidae)

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## ABSTRACT

The Tasmanian terrestrial pulmonates *Cystopelta petterdi* Tate, 1881 and *Cystopelta bicolor* Petterd & Hedley, 1909 are redescribed and neotypes erected. A diagnosis of *Cystopelta* Tate, 1881 is provided.

## INTRODUCTION

Two species of *Cystopelta* Tate, 1881 are recorded from Tasmania, *C. petterdi* Tate, 1881 and *C. bicolor* Petterd & Hedley, 1909. Due to the range of superficial variation identification of these species has been uncertain. No recognizable type material is known although dried possible syntype specimens of *C. bicolor* exist in the Australian Museum and the Queen Victoria Museum. This material does not constitute effective type material (B.J. Smith, pers. comm.).

This paper describes the anatomy of *C. petterdi* and *C. bicolor*, erects neotypes and provides a diagnosis of the genus *Cystopelta*. Tate's (1881) description of the genus clearly established the external appearance of a shell-less animal with a distinct visceral mass protected by an "inflated or bladder-like shield". This shield is apparently a modification of the mantle and possibly lappets now indistinguishable. The animal is a semi-slug as defined by Tillier (1984).

## THE FAMILY

The first record of a family name is that of Cockerel (1891) who introduced Cystopeltinae on the basis of narrow teeth and "ribbed jaw". The "ribs" are in fact folds. Iredale (1937) gave the group family status and this was accepted by Kershaw (1955), McMichael & Iredale (1959), Altena & Smith (1975), Smith (1977, 1979), Smith & Kershaw (1979, 1981) and Bishop (1981). Cystopeltinae was used by Thiele (1931), Baker (1956), Zilch (1960) and Burch (1976).

These decisions on family status were based on anatomical studies by Hedley (1890b) and Davies (1912) dealing with material from New South Wales and Victoria. Hedley later (1891) remarked that he could not separate Mt Kosciusko and Launceston specimens he dissected. Thiele's (1931)



description was based on radula and genital data. The family is more complex than anticipated and definition is beyond the scope of this paper which continues studies previously briefly reported (Kershaw, 1957). The work suggests a possible second genus in Tasmania.

The Cystopeltidae are endemic to eastern Australia from southern Queensland to Tasmania. Brief descriptions and distributional data are provided by Smith & Kershaw (1981). Bishop (1981) referred to food and habitat. Recognition of the species level taxa of Davies (1912) and Iredale (1937) was delayed by Smith & Kershaw (1979, 1981) due to the need for authentic material from Tasmanian type localities.

## MATERIAL AND METHODS

The neotypes proposed in this paper are lodged in the Tasmanian Museum. This study is based on material lodged in the Tasmanian Museum (TM), the Museum of Victoria (NMV), the Queen Victoria Museum (QVM) and the author's collection to be lodged in these museums. Voucher material is lodged in these museums and the Australian Museum (AM) Sydney.

Grid references provided refer to the 1:100 000 Topographic Survey, Tasmania, Sheet 8315 (St Patricks), 8015 (Hellyer) and 7915 (Arthur River). All dissections were done by the author using either a Zeiss or a Wild dissecting microscope with drawing attachment. Drawings and photographs are by the author. Scanning electron micrographs of the radulae are by Adrian Daniell of La Trobe University.

Material dissected includes 40 specimens of *C. petterdi* together with many others from Tasmanian and Victorian localities. Only three specimens of *C. bicolor* from the type locality vicinity and at least one from central Tasmania have been available for dissection. Similar animals not dissected occur in Victoria.

The nomenclature used for the genitalia in this study is based on that adopted by Tompa (1984).

## CYSTOPELTA TATE, 1881

Type species by monotypy, *Cystopelta petterdi* Tate, 1881. Diagnosis: Semi-slugs in which the shell may be absent but is usually reduced to a thin horny membrane adhering to the distinct visceral hump enclosed beneath a flexible wrinkled mantle-shield below which the foot protrudes noticeably only in the crawling animal. A pedal groove (Fig.4) is clearly visible above the wide vertically lobed or almost smooth sole margin. There is no dart sac, penial verge, flagellum or caecum but an epiphallus is present. The atrium is elongate with an internal coiled duct fused to the atrial wall. The oviducal pore within the vagina (Figs.12 and 18) is a variably prominent cone shaped process which is extrudable and possibly has a stimulatory function. The genitalia are extruded during copulation.

The relatively short tail (Figs.4, 5 and 16) is truncate and recessed with a distinct caudal gland surmounted by a caudal horn above which is a small diamond shaped process. The short foot cavity which has the posterior margin anterior to the stomach, contains the anterior oesophagus and salivary glands overlapping the basal gonoduct lobe. The tentacle and buccal retractors insert with a reduced columellar muscle above the posterior margin. The right ocular tentacle passes above the vagina (Fig.16)

The jaw (Fig.6) is very thin, flexible, capable of small folds and transversely marked by very fine very close lirae variably visible cut by faint longitudinal striae.

The radular teeth (Figs.20-33) are mounted on very long narrow basal plates. The central tooth is unicuspid or tricuspid with lateral cusps markedly anterior to the elongate median cusp. The lateral teeth are tricuspid or multicuspid. The marginal teeth are multicuspid and become more elongate narrow with the cusps of outer marginals more or less prominent elongate.

### Generic features

The conspicuous oviducal cone-shaped papilla observed in the vagina, here termed an-

'ovipositor' (Figs.12 and 18) is believed confined to this genus. It is distinct from the inconspicuous pore papilla of certain other animals. Mating observations supported by those of Daniell (in litt., 1985) suggest that the organ has a role during copulation. The genitalia are extruded during copulation, the parts involved depending on the role of the individual animal as male or female. The atrium upon extrusion forms a flexible sheath, the 'atrial sheath'. The contained coiled duct, here termed the 'atrial duct', straightens with extrusion but remains within the sheath. Another example of genital extrusion in the case of *Partula affinis* Pease was described by Kondo & Burch (1979).

Evolution toward slug morphology has resulted in modification of superficial form as well as anatomy so that convergence tends to restrict factors of taxonomic value. However the genitalia display features which have species, generic and family value. In *Cystopelta* the prominent vaginal papilla and the fusion of the atrial duct at the gonopore and internally are here considered diagnostic features. A distinct group exists in which the oviducal papilla is greatly reduced and the atrial duct is only partly fused or not fused. These components are not continuous with the vaginal and penial chambers as in typical *Cystopelta*.

### Supragenetic features

The foot structure and kidney structure places the animal in the Aulacopoda Sigmurethra (Pilsbry, 1946; Solem, 1959) although the ureter is much modified and the writer cannot distinguish a secondary component. The primary ureter is a distinct duct curving from the apex postero-dorsally (Fig.7) (Davies, 1912) across the kidney into the pneumostome chamber adjacent to the anus and pneumopore. On the basis of radula factors the animal belongs to the Limacacea (Solem, 1959; 1978). The globular ovotestis has subcylindrical component lobules radiating from the central ovotestis duct (Fig.9) to be capped externally with white distinct apices. The gonoduct is distinguished to a significant degree by a structural division into apical and basal lobes from which the oviduct and vas deferens branch as usual (Figs.11 and 17). The apical lobe contains a capacious lumen across which the path of the uterus appears curved (Fig.13). At first this was considered distinct from the male duct but further observation has revealed a fairly brief region of commonality. The basal lobe is a complex of elements which appear discrete but the degree to which the ducts are common or separate must await study at the family level.

### Relationships

There is no clear association with Australian genera studied as yet. The marginal teeth suggest a relationship to the helicarionid snails which appears less apparent in Tasmanian *Helicarion* (Dartnall & Kershaw, 1978; Kershaw, 1979). Urocyclid forms (Solem & Van Goethem, 1974) do suggest that marginal teeth denticles should be considered. The series of cusps present on *C. bicolor* marginals may indicate a common ancestral form for *Cystopelta* and an helicarionid assuming that in the latter the marginal cusps have modified. But this is no more than supposition.

Hedley (1890a; 1890b) and Iredale both suggest a resemblance to *Helicarion* and further comparisons can be made in tooth number (Solem, 1976). Comparisons can be made with genera of the Euconulidae (Baker, 1941) or the Microcystinae (Baker, 1938) in the presence of an epiphallus with no flagellum, a caudal foss and horn and a simple spermatophore. However there are also resemblances with the Arionacea when comparisons are made on the basis of the work of Solem (1982) especially in the epiphallus structure (Climo, in litt., 1986) in the Charopidae.

## **CYSTOPELTA PETTERDI TATE, 1881**

Neotype: One specimen TM E16318 (Figs.1 and 2) collected by A. Daniell and R.C. Kershaw, 21 May 1984, 1 kilometre west of Cataract Gorge near Launceston, Tasmania, grid 508800mE 5411650mN about 100 metres above sea level.

### Description

External: The animal (Fig.1) of medium size is 37mm long reaching to about 40mm fully extended. The mantle-shield is variously coloured brown to dark brown or greyish with mottles and often lines on the flanks. The whole fades to greyish shades with the shield contracting in preservative

(Fig.2). The body is pale grey to off white but the foot margin and tail may be brownish, bluish or grey. The upper tail ornament is a tubercular surface defined into a chevron pattern accentuated by brown lines separating the dense mottle of minute pale spots also present on the shield.

### **Anatomy**

The jaw (Fig.6) is yellow, very thin and flexible and often variably crumpled into small folds.

The radula (Fig.20) of about 96 rows of minute teeth has some 400 teeth per row. The teeth are narrow elongate and are mounted anteriorly on elongate basal plates. There are about 25 or 26 lateral teeth which appear to grade into the marginals but variation is present.

The central tooth (Fig.21) is strongly hooked unicuspid, the long cusp having a scalloped curve to the basal plate which is narrowed at its extremities, strongly buttressed below the hook and laterally tapered outward. Anteriorly the plate is short and slightly hooked, posteriorly it is elongate. The first lateral teeth (Fig.21) are tricuspid with a rather narrow pointed very elongate mesocone, a much narrower endocone reaching to about mid-point and a short anterior ectocone. The stump of a possible second ectocone can be seen on one tooth. Clearly longer than the central tooth these teeth are laterally angled and curved upward posteriorly.

The subsequent laterals (Figs.22 and 23) have the same pattern but there is an added elongate narrow endoconal cusp on some teeth between the prominent endocone and the mesocone, which varies in apparent length. This cusp becomes longer and stouter than in earlier laterals. Viewed laterally the mesocones are seen to be hooked and the endocones extend more than half the tooth length. The cusps are elongate and pointed when free of wear. Mostly there is one clear long ectocone but there are stubs of a second.

The transition (Figs.24 and 25) to the marginals is not precise but the second endocone becomes more prominent and a second ectocone bolder more frequent. This is noticeable near an aberrant tooth (Fig.25), no more than a stump with one cusp about one third the distance from the central tooth. Here most teeth have one long ectocone. The viewing angle to the right reveals the sides of the plates. The second ectocone is more commonly visible. The marginal teeth (Fig.26) have two elongate ectocones and the endocones are more elongate although variable. The outer endocone is distinctly prominent and almost as long as the mesocone. The basal plates appear narrower more elongate.

Variation is indicated between the several radulae studied. A feature is the interrow junction which is prominent and raised like rope (Fig.23) in some areas or ridged (Fig.22) but may be barely prominent (Fig.21). In one case the teeth are strongly worn but the plate structure is clear and the elongate central tooth is almost hidden by the laterals.

### **Reproductive anatomy**

Apical genitalia (Figs.11 and 13): The globular ovotestis is pale cream in colour tending to brownish in mature animals. The short hermaphroditic duct is enclosed within a thin transparent sheath and becomes kinked with the development of seminal vesicles. It enters the somewhat sub-ovoid shaped albumen gland laterally to junction with the talon below the surface. The talon (Fig.13) is about 1 mm long with a distinct apical lobe usually just protruding from the albumen gland surface. The talon narrows sharply to the carrefour (Fig.13) which is narrow transverse then sharply angled into the oviduct-prostate junction. The oviduct enters the apical lobe of the uterus as a pale distinct duct initially apparently distinct from the prostate. The ducts become common briefly prior to the inter-lobe neck. The uterine lobe expands and becomes somewhat translucent with female sexual maturity but retains its globular shape. The basal lobe barely expands but also changes colour. The prostate (Fig.11) is very pale cream barely visible in immature animals but becomes clear, wider and a deeper cream colour with male maturity. It empties to the vas deferens within the basal lobe.

Terminal Genitalia: The free oviduct (Fig.11) is either attached to or separate from the vas deferens at the point of bifurcation at the basal gonoduct lobe. It passes across the bursa duct opposite to the vas deferens as a narrow duct of 7 to 9mm length to the oviducal pore without discernable glandular tissue. The pore enters a swollen lumen within the cone-shaped ovipositor which consists



of a sleeve of 'skin' fused to the vagina wall apically and having a concertina like structure of ridges providing for expansion when extruded through the atrium and atrial duct. The vagina (Fig.12) is a swollen chamber some 3mm long resting almost transversely above the atrium and opening opposite the bursa duct pore.

The vas deferens (Figs.11 and 12) is a thin coiled duct about 9 to 12mm long passing across the bursa duct surface before expanding into the epiphallus which is a short but variable section of the duct expanding to the male pore. Internally the epiphallus is lined with two bold high narrow white pilasters with a narrow low pilaster between (Fig.12). There are very fine irregular low lateral ridges. The structure passes basally into very low ridges cut by transverse grooves within a briefly expanded section which narrows then expands into a vestibular area lined with subrounded pustules which narrows abruptly into the male pore situate adjacent the penial retractor attachment to the penial chamber.

The penial chamber (Figs.11 and 12) is a cylindrical lumen with or without an obvious rounded external swelling adjacent the retractor, capacious and weakly lined with longitudinal grooves and faint close ridges. Apically a variably ornamented and swollen process (Fig.12) is situated on the wall and when fully expanded is responsible for the external swelling. This process adjacent the male pore may have a stimulatory and/or diverticular function as the internal pouch may be filled with breakdown material such as occurs in the bursa duct lumen. Variations in the structure of the pore region have been seen. The penial retractor (Figs.11 and 12) is a short strong white tubular muscle arising from the ventral lung epithelium on the left side (Fig.5), attached to muscular epithelium from the bursa duct and then passing to the apical penial chamber surface broadly but superficially.

The bursa copulatrix (Fig.11) is a small globular body separated from its duct by a constricted narrow hiatus through the foot diaphragm which also constricts the neck between the two uterine lobes. The muscular epithelium to the penial retractor attaches at this point and is part of the diaphragm tissue enabling the retractor to control both penial and bursa activity. The bursa duct is capacious, weakly lined basally and receives spermatophore from which very little reaches the weak copulatrix. A spermatophore has been observed protruding from the pore into the penial chamber.

The spermatophore (Fig.8) is a yellowish transparent 6mm long capsule obtusely truncate anteriorly, curving to a fine point posteriorly.

The atrium is an elongate pouch opening at the gonopore, which contains the coiled atrial duct (Figs.10, 11 and 12) and is extruded as an atrial sheath containing the duct during copulation. The atrial duct is lined with many (about 36) very fine ridged folds which are continuous with the basal penial and vaginal chambers. The ornament is very variable and may be weak or clear but is often seen as a series of major folds with several minor folds between. The sheath normally protrudes following preservation.

### The type locality

The type locality was identified by Hedley (1891) who collected there with Petterd. The neotype site is about a kilometre away due to suburban development. The site and habitat will be described elsewhere (Kershaw, ms.). Voucher material: One specimen AM C147139 collected A. Daniell and R.C. Kershaw, 21 May, 1984; two specimens QVM442 1985/8/1 (whole), QVM443 1985/9/2 (dissected) collected R.C. Kershaw 28 October, 1984, all from the neotype locality. Two specimens NMV F52162 and one specimen (dissected) NMV F52163 collected R.C. Kershaw 16 August, 1975 from adjacent the neotype locality, grid 508900mE 5411600mN.

## **CYSTOPELTA BICOLOR PETTERD & HEDLEY, 1909**

Neotype: One specimen TM E16804 (Fig.3) collected R.C. & W.M. Kershaw, 7 Jun 1986, adjacent road to Magnet Mine, west of Waratah, western Tasmania, grid 370400mE 541090mN about 500 metres above sea level.

### Description

External: The animal (Fig.3) of medium size is 33mm long. The mantle-shield is brown with grey brown patches mainly on the flanks and is produced posteriorly. The foot is dull green in life fading to pale cream in preservative, the head almost white and the tentacles pale cream. The neck is marked with shallow transverse grooves. The tail surface pattern of tubercles and grooves arranged as a chevron is barely accentuated. The sole margin is variably weakly lobed. The caudal mucus is green.

### Anatomy

The jaw is very thin as in *C. petterdi* but coloured white on the upper arch surface, cream centrally and brownish on the lower margin.

The radula (Fig.28) curves to a shallow 'V' centrally. There are at least 300 minute narrow elongate teeth mounted posteriorly on elongate basal plates. Centrally about three fifths of the plate are anterior to the tooth but a gradual change occurs towards the margins revealing more of the plate posteriorly. The plate length increases slightly at first then the plates curve and twist in the transitional area so that the typical pattern is derived. Anteriorly the tooth arises from the plate as a very thin ridge expanding into the elongate mesocone.

The central tooth (Fig.29) is tricuspid with a minute denticle adjacent the elongate ectocones. The mesocone is elongate and barely or not hooked. The lateral teeth (Fig.30) are multicuspid with a relatively broad elongate mesocone, 2 or 3 endocones and 2 or 3 ectocones. The ectocones decrease in size to a very small cusp anteriorly. The outermost endocone is prominent. Four cusps sometimes appear or only one, possibly due to wear. There are about 50 lateral teeth to the transitional region where the plates become narrow and curve anteriorly.

The latero-marginal teeth (Fig.31) are distinctly smaller with the plates progressively curving and twisting anteriorly with an increasing proportion of the plate appearing posteriorly. The mesocone is short and narrow with 2 prominent endocones and 3 or 4 ectocones.

The marginal teeth (Figs.32 and 33) are much narrower and shorter with the mesocone about half the length of that of the laterals reducing to about one-third at the radula margin. The mesocone has become distinctly hooked (Fig.33). There are similar endocones arranged adjacent to the mesocone and 4 or 5 ectocones in a series anteriorly. The proportion of the basal plate now visible is obvious while anteriorly the plate is strongly twisted. (Fig.33).

### Reproductive anatomy

Apical genitalia (Figs.14 and 17): The globular ovotestis is small greyish pale cream. The albumen gland is large and pale orange. The apical lobe of the talon does not protrude from the surface of the gland. The talon is 0.9mm long, white in colour and enters the carrefour through a relatively elongate narrow duct. The carrefour is large, somewhat elongate, barely transverse and almost obtusely angled into the oviduct-prostate junction (Fig.14). The oviduct expands to enter the apical uterine lobe which is swollen and somewhat translucent with a large flattened internal lumen. The prostate (Fig.14) is white in the Magnet animal and pale cream in an animal from the Murchison Highway.

Terminal genitalia (Fig.17): There is a superficial resemblance to *C. petterdi* but the free oviduct is longer, about 10 mm or more. The vagina (Figs.17 and 18) is a swollen, short, 2mm chamber resting at a slight angle clearly above the atrium and opening distinctly above the bursa duct pore. The ovipositor (Fig.18) closely resembles that of *C. petterdi* although smaller in the animals dissected.

The vas deferens (Fig.17) is a thin short coiled duct 5.5 to 6.5mm long which passes across the bursa duct surface opposite the free oviduct and expands rather abruptly into the strongly expanded transparent epiphallus which joins the penial chamber laterally. Internally the epiphallus ornament is of 4 strong pilasters occupying most of the lumen with a very short lateral pilaster and traces of transverse ridges adjacent the male pore (Fig.18). The pore opens into a small pustular lined chamber from which the penial chamber opens over a distinct ridge.

The penial chamber (Fig.18 and 19) is cylindrical short and narrow without an internal or external swollen process adjacent the pore. It is lined variably with transverse and longitudinal fine ridges,

most complex near the bursa duct pore, which pass into the atrium and vagina. The penial retractor (Figs.16, 17 and 18) is a thin white muscle 3 to 4.5mm long arising from the lung diaphragm well to the left side near the heart. It appears to have no connection to the bursa duct and passes to the apical penial chamber in the male pore region.

The bursa copulatrix (Fig.17) is small with a constricted neck to its duct as in *C. petterdi*. The neck is attached to the foot diaphragm epithelium. The duct is capacious and enters the atrium at the base of the penial chamber but in this animal the atrium appears very shallow on the male side with little significant space between the pore and gonoduct site.

The spermatophore (Figs.15 and 19) is small, white and only slightly narrowed posteriorly. It was found protruding through the male pore (Fig.19).

### The type locality

Petterd & Hedley (1909) state that the habitat is the Magnet Range and the Upper Pieman River. The type locality is here restricted to the Magnet area. The site and habitat will be defined and described elsewhere (Kershaw,ms.). *Cystopelta bicolor* is a rainforest species.

Possible syntype material: Two dried specimens AM C27807. One dried specimen QVM409 1983/9/4.

Voucher material: Three specimens collected R.C. & W.M. Kershaw all dissected. One specimen QVM427 1986/9/30 collected at neotype locality. Two specimens QVM428 1986/9/31 a and b collected 9 June, 1986 adjacent the Murchison Highway north of Hellyer Gorge, grid 382600mE 5430600mN, in coils of bark, rainforest north of neotype locality.

### Remarks

The specimens from near the type locality are very uniform in appearance. Two specimens from central Tasmania had a brighter green foot as stated by Petterd & Hedley (1909) for their material. Of the four specimens dissected three are considered adult and two of these are from or close to the type locality. Most other forms of *Cystopelta* vary in colour a good deal but animals with a green foot are not often seen in Tasmania.

The most significant features distinguishing *C. bicolor* excluding the foot colour, are the radula and the terminal genital features. Evidence from the range of forms so far studied support the weight given here.

### Species comparison

	<i>C. petterdi</i>	<i>C. bicolor</i>
Radular teeth:		
Central	monocuspid	tricuspid
Lateral	most tricuspid	usually 4 cusps
Marginal	2 ectocones	4-5 ectocones
Endocones	unequal	equal
Basal plates	not twisted	twisted
Jaw	yellow	white
Foot		
Margin	lobed	barely lobed
Colour	not green	green
Mucus	yellow green	green
Apical genitalia:		
Carrefour	immersed	bulging
Talon-carrefour	short	long
Carrefour-uterus	acute	obtuse
Terminal genitalia:		
Free oviduct	short	long
Vas deferens	long	short
Epiphallus	3 pilasters	4 pilasters



Epiphallus-penis	apical	lateral
Vagina-bursa duct	opposite	not opposite
Penial process	present	absent
Atrial duct	folds thin	folds bold
	not lined	lined
Spermatophore	tapered	barely tapered
Retractor muscle	thick	thin

The penial retractor of *C. bicolor* arises distinctly nearer the left flank than that of *C. petterdi*.

## ACKNOWLEDGMENTS

Particular gratitude is due to Adrian Daniell for the radula micrographs and continued interest. Dr B.J. Smith has provided valuable discussion and field assistance. Drs A. Solem and F. Climo provided helpful discussion. I thank Miss Alison Green and Mrs E. Turner (Tasmanian Museum), Mr R.H. Green and Miss K. Dimmack (Queen Victoria Museum), Dr R. Mesibov, Mr P. Duckworth and their colleagues (Forestry Commission) for specimens, literature and interest. My wife Winifred has patiently corrected mistakes and provided invaluable field assistance. Gratitude is due to the Trustees of the Science and Industry Endowment Fund for continued support.

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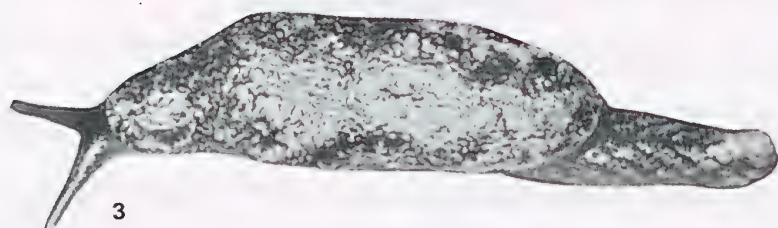


FIGURE 1. *Cystopelta petterdi* Tate. Neotype. Live length 37mm. FIGURE 2. *Cystopelta petterdi* Tate. Neotype preserved 26mm. FIGURE 3. *Cystopelta bicolor* Petterd & Hedley. Neotype. Live length 33mm.



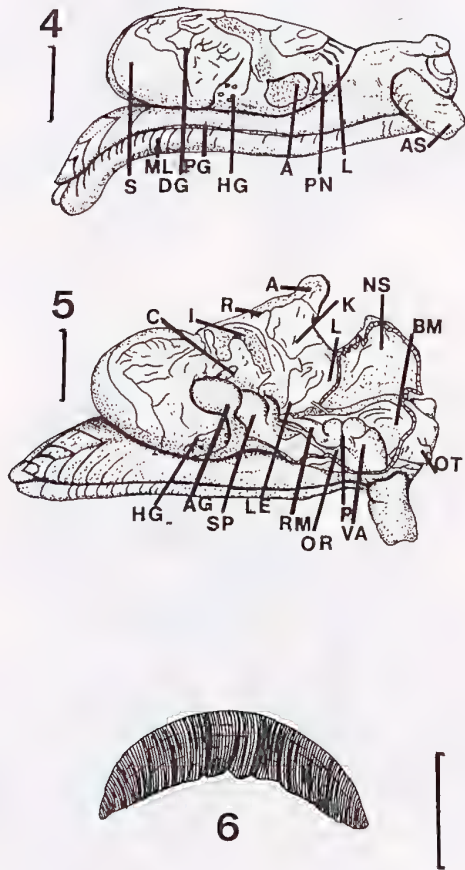


FIGURE 4. *C. petterdi*: lateral aspect of animal with shield removed. Scale line 5mm.  
FIGURE 5. *C. petterdi*: partly dissected showing ventral aspect of pallial organs and foot organs *in situ*. Scale line 5mm.  
FIGURE 6. *C. petterdi*: jaw. Scale line 1mm.

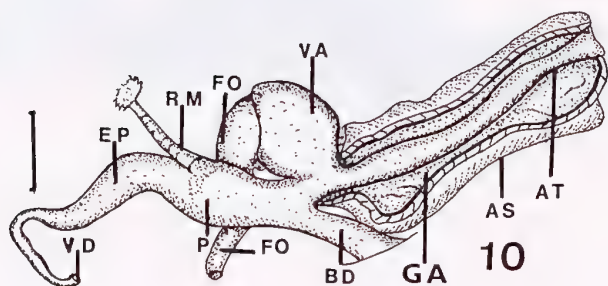
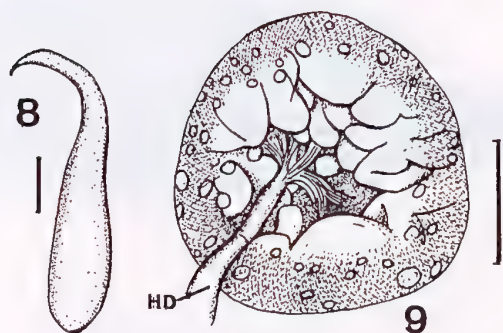
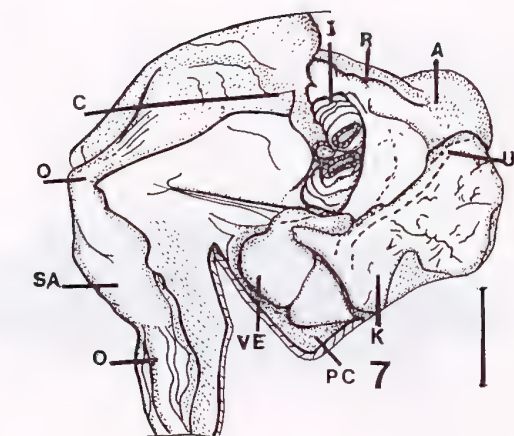


FIGURE 7. *C. petterdi*: Kidney (K), pericardium (PC), intestine (I) coils cut and salivary gland (SA) exposed. Scale line 2mm.

FIGURE 8. *C. petterdi*: spermatophore. Scale line 1mm.

FIGURE 9. *C. petterdi*: ovotestis internal structure. Scale line 1mm.

FIGURE 10. *C. petterdi*: atrial sheath (AS) opened exposing atrial duct (AT). Scale line 2mm."

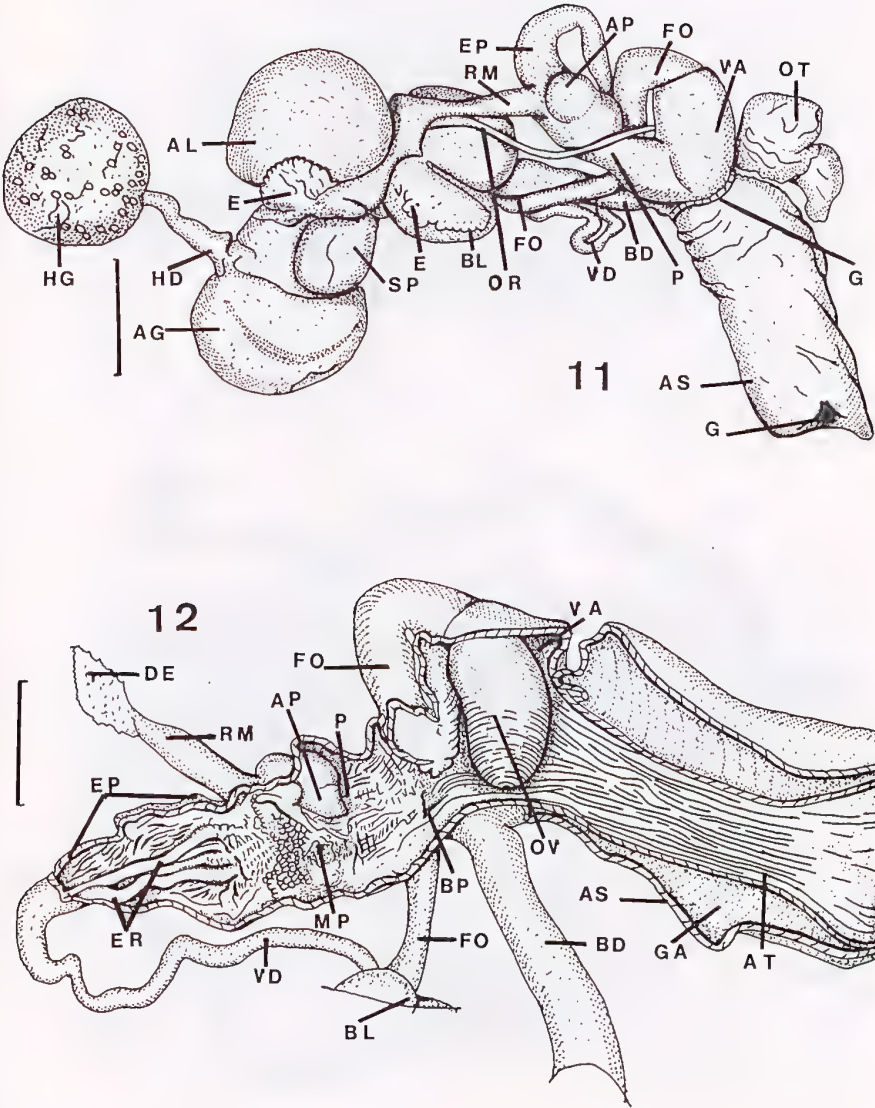


FIGURE 11. *C. petterdi*: genitalia as lifted from body of animal. Scale line 3mm.  
FIGURE 12. *C. petterdi*: internal detail of terminal genitalia showing atrial duct (AT), ovipositor (OV), penial chamber (P), male pore (MP) and structure of epiphallus (ER). Scale line 2mm.



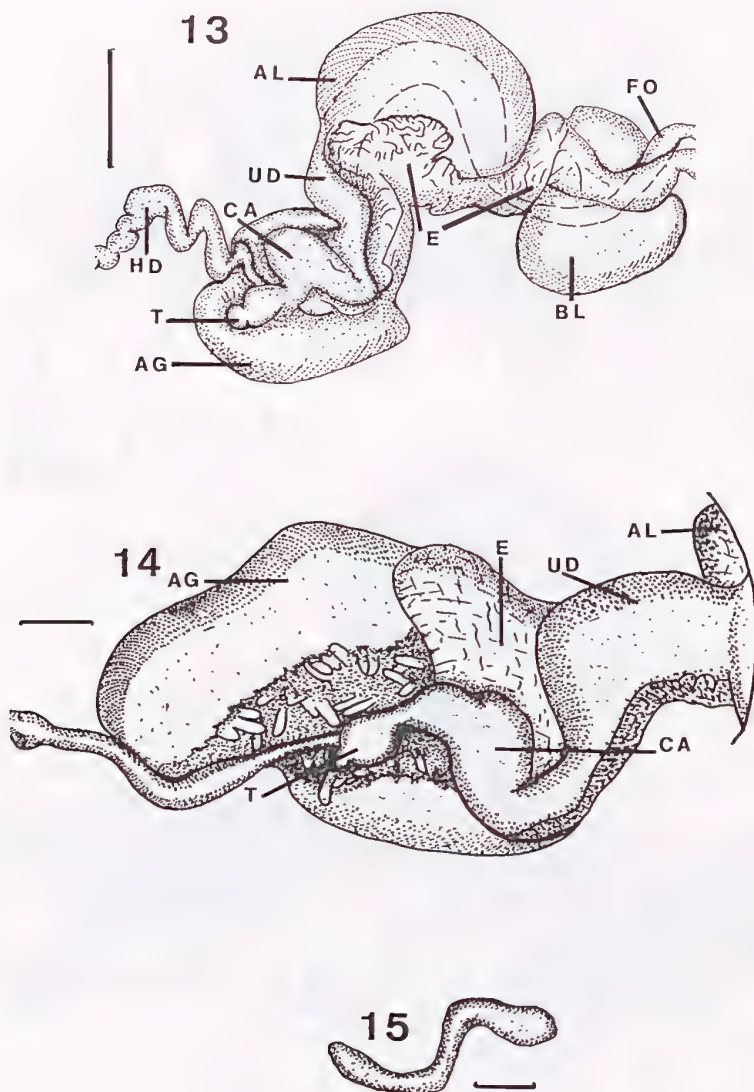


FIGURE 13. *C. petterdi*: apical genitalia showing relationship between talon (T), carrefour (CA), oviduct (UD), prostate (E) and lobes of uterus (AL, BL). Scale line 2mm.

FIGURE 14. *C. bicolor*: apical genitalia showing relationships between talon (T), carrefour (CA), oviduct (UD), prostate (E) and apical lobe (AL) of uterus. Scale line 1mm.

FIGURE 15. *C. bicolor*: spermatophore. Scale line 1mm.

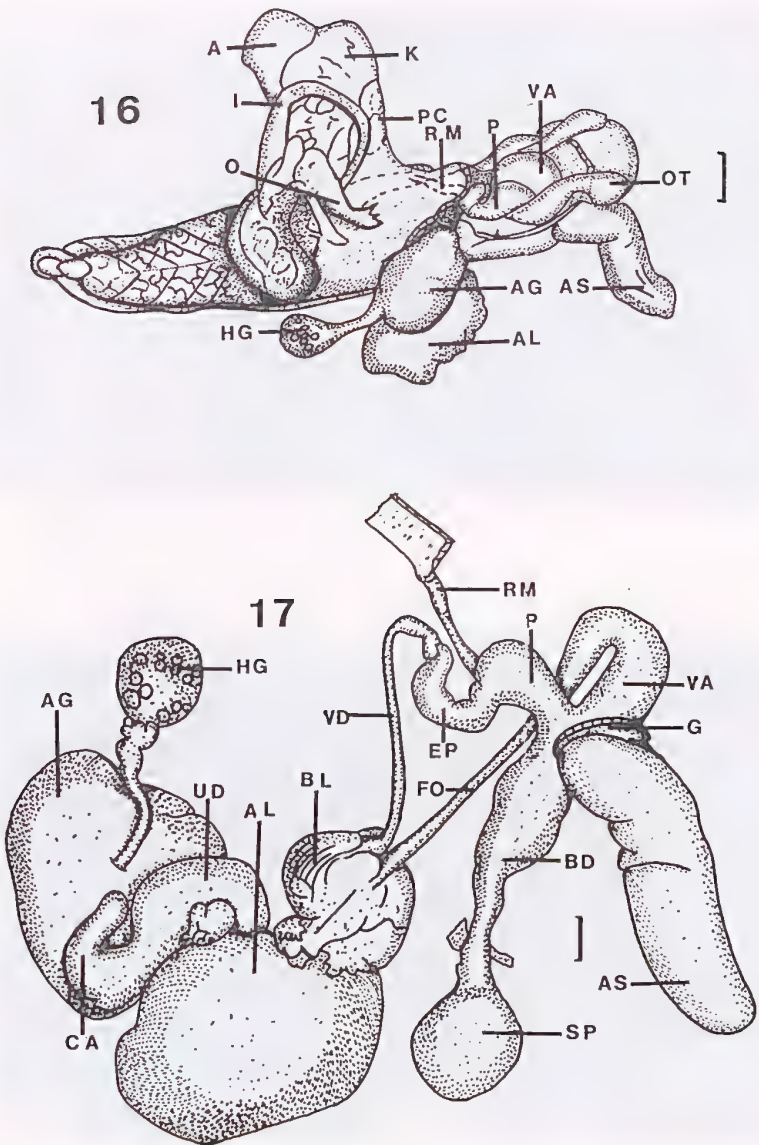


FIGURE 16. *C. bicolor*: animal partly dissected showing ventral pallial organs, path of penial retractor (RM) and optical tentacle (OT). Scale line 2mm.

FIGURE 17. *C. bicolor*: genitalia set out for dissection showing proportions. Scale line 1mm.

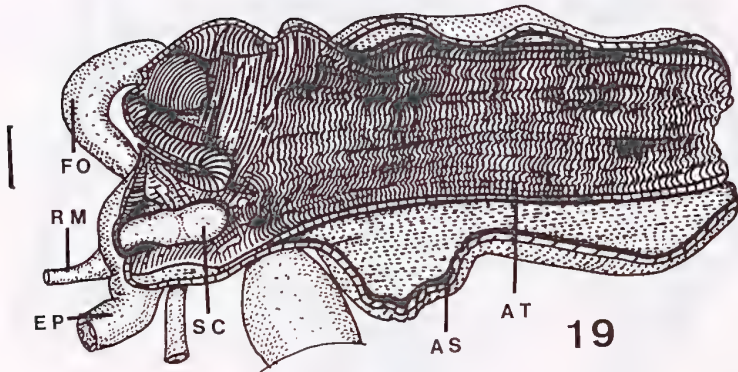
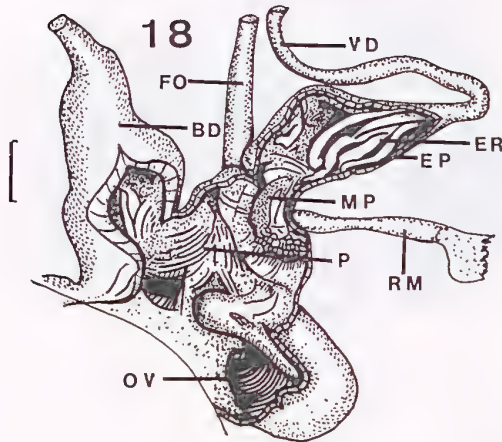


FIGURE 18. *C. bicolor*: internal structure of epiphallus (EP), penial chamber (P), male pore (MP), bursa duct (BD) pore and ovipositor (OV). Scale line 1mm.

FIGURE 19. *C. bicolor*: internal detail of atrial duct (AT) and vagina (VA) with spermatophore (SC) protruding from epiphallus (EP). Scale line 1mm.



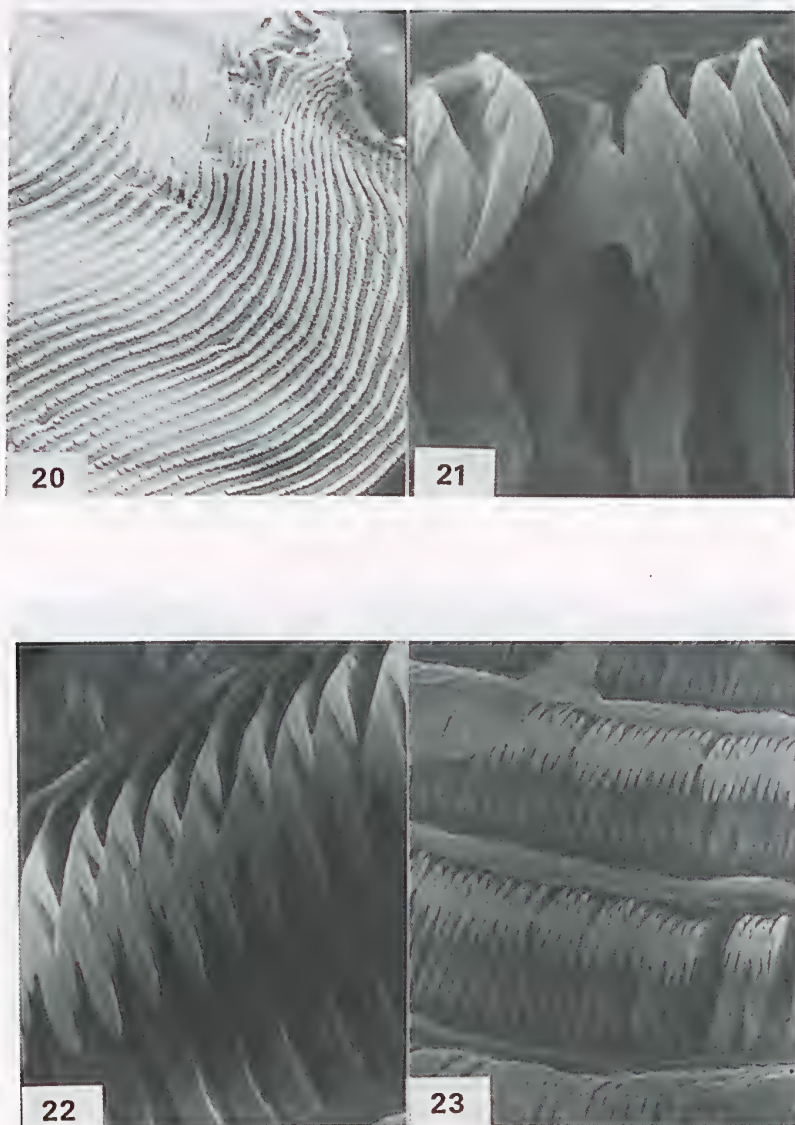


FIGURE 20. *C. petterdi*: radular teeth at X50.

FIGURE 21. *C. petterdi*: central and adjacent lateral teeth at X1320.

FIGURE 22. *C. petterdi*: lateral teeth showing added ectocone at X3300.

FIGURE 23. *C. petterdi*: lateral teeth at X600 showing elongate basal plates.

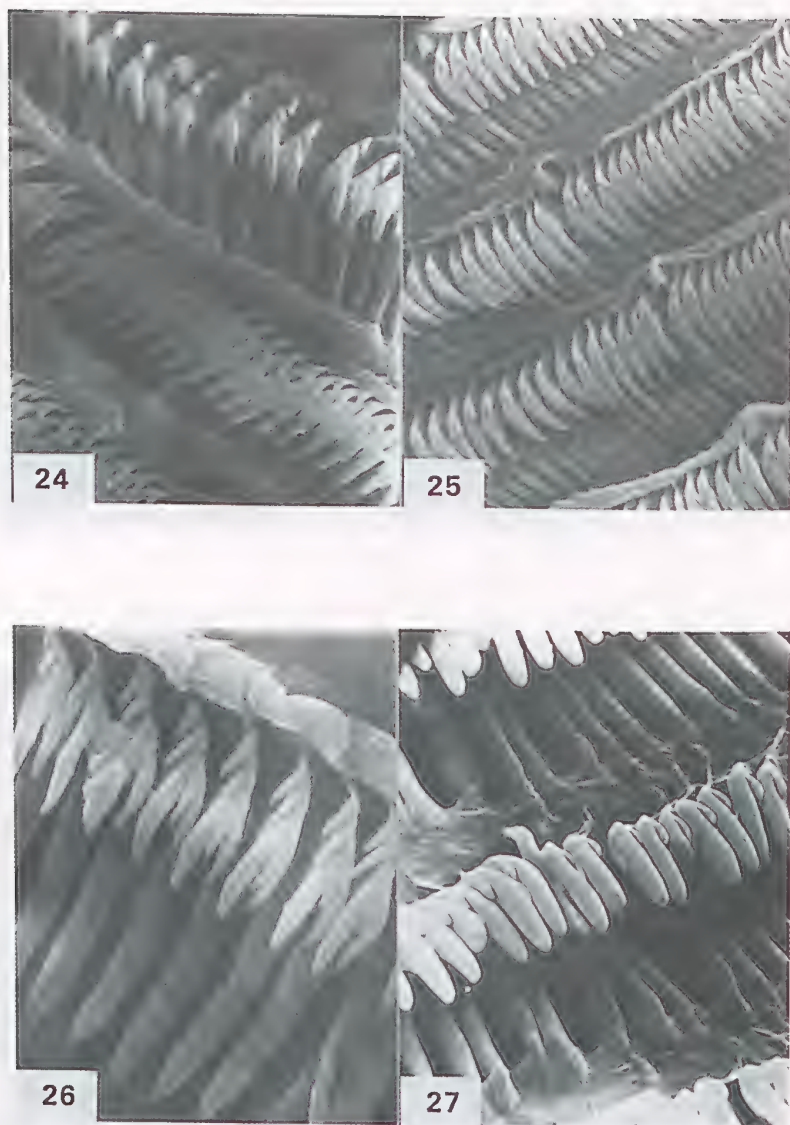


FIGURE 24. *C. petterdi*: latero-marginal teeth at X1500. The additional cusp has become more frequent.

FIGURE 25. *C. petterdi*: transitional teeth at X580 showing an aberrant tooth.

FIGURE 26. *C. petterdi*: marginal teeth at X3000 showing 5 cusps on all teeth and the prominent endocone.

FIGURE 27. *C. petterdi*: strongly worn central and lateral teeth at X3200.

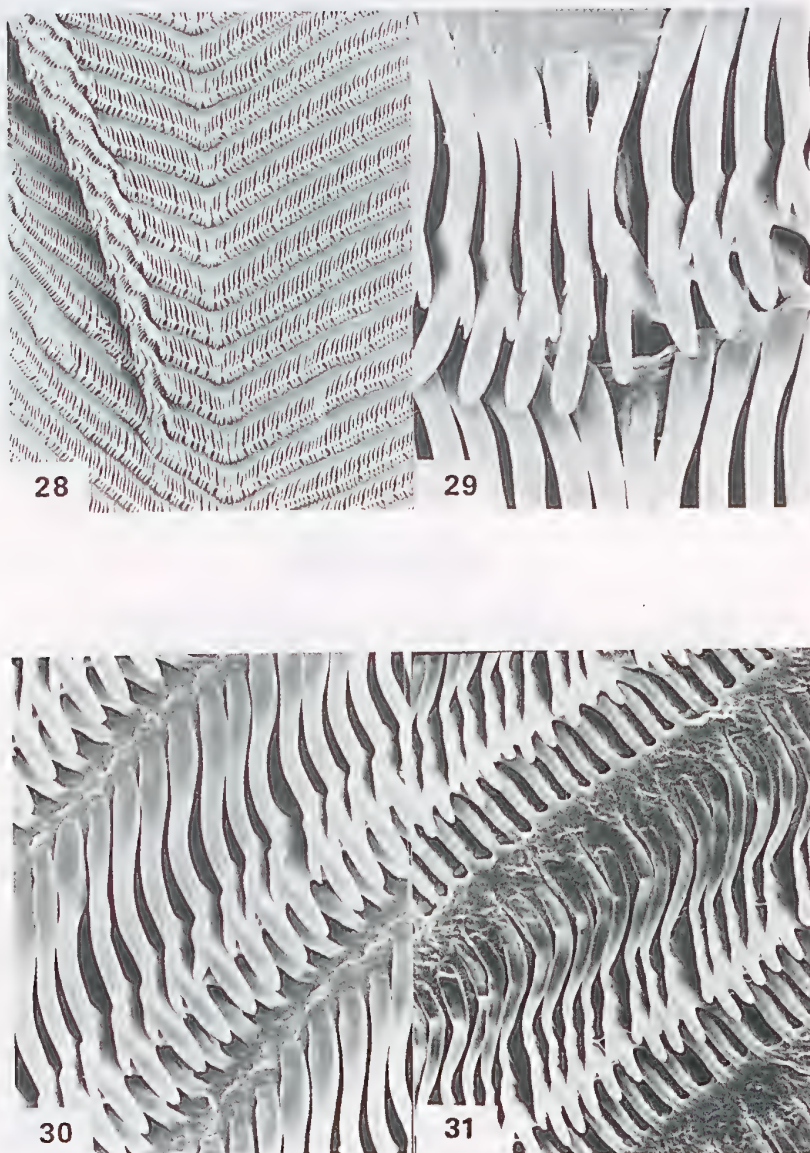


FIGURE 28. *C. bicolor*: radular teeth at X100.

FIGURE 29. *C. bicolor*: central teeth and adjacent lateral teeth at X1000.

FIGURE 30. *C. bicolor*: lateral teeth at X800. Posterior basal plates becoming more exposed.

FIGURE 31. *C. bicolor*: latero-marginal teeth at X800. Basal plates are now curved.



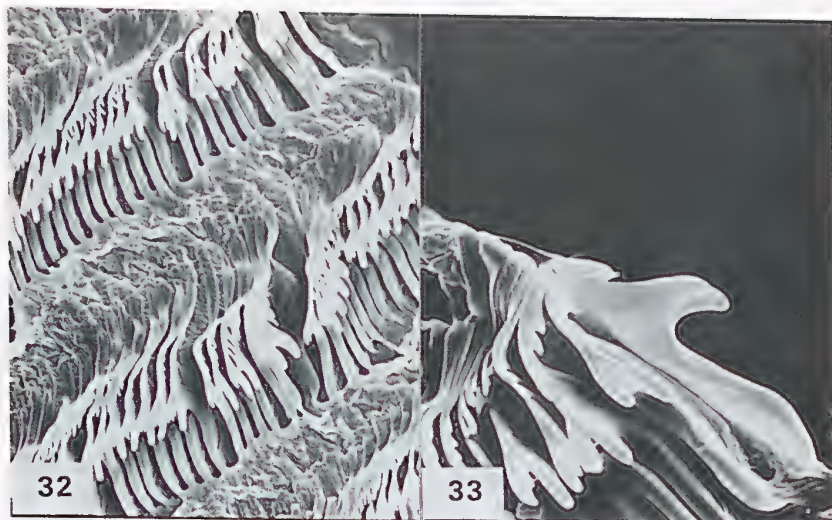


FIGURE 32. *C. bicolor*: marginal teeth at X730. Basal plates curved and twisted.

FIGURE 33. *C. bicolor*: marginal teeth - lateral view at X1800.

## ABBREVIATIONS

A- anus;	AG- albumen gland;
AL- apical lobe of uterus;	AP- apical penial process;
AS- atrial duct sheath;	AT- atrial duct;
BD- bursa duct;	BL- basal lobe of uterus;
BM- buccal mass;	BP- bursa duct pore;
C- crop;	CA- carrefour;
DE- diaphragm epithelium;	DG- digestive gland;
E- prostate;	EP- epiphallus;
ER- epiphallic pilasters;	FO- free oviduct;
G- gonopore;	GA- genital atrium;
HG- ovotestis;	HD- hermaphroditic duct;
I- intestine;	K- kidney;
L- lung;	LE- lung tissue;
ML- sole margin lobes;	MP- male duct pore;
NS- neck skin;	O- oesophagus;
OR- ocular retractor muscle;	OT- ocular tentacles;
OV- ovipositor, oviducal pore;	P- penial chamber;
PC- pericardium;	PG- pedal groove;
PN- pneumopore;	R- rectum;
RM- penial retractor muscle;	S- stomach;
SA- salivary gland;	SC- spermatophore;
SP- bursa copulatrix;	T- talon;
U- ureter;	UD- uterus;
VA- vagina;	VD- vas deferens;
VE- ventricle	

## Phylogenetic systematics and zoogeography of Australian nudibranchs

### 1. Presence of the aeolid *Godiva quadricolor* (Barnard) in Western Australia

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#### ABSTRACT

The aeolid *Godiva quadricolor* (Barnard, 1927) is newly recorded from Australia on the basis of a population in southwestern Australia. It was first observed about 1980 and it is apparently presently restricted to the Fremantle-Cockburn Sound area. Shipping offers the most plausible explanation for transportation of the original stock from southern Africa. A complete anatomical description is provided to enable its future recognition. The genus *Godiva* Macnae, 1954, which is redefined and its scope restricted to embrace two (probably three) species, is relatively advanced within both the superfamily Aeolidioidea and family Facelinidae. At present the penial spine is the only character that can be identified as an autapomorphy, but it is suggested that, in fact, a suite of apomorphies relating to the penial spine and jaw ornamentation do exist. Eight other aeolids that have been included in *Godiva* at one time or another are discussed and excluded. Although apparently derived from the Facelinidae Vayssi re, 1888, the Glaucidae F russac, 1822 deserves separate familial ranking because of numerous apomorphies acquired during the evolution of its novel pleustonic life style. Phidianidae Odhner in Franc in Grass , 1968 is confirmed as a junior synonym of Facelinidae.

#### INTRODUCTION

Whilst investigating the intertidal biota encrusting the beacon pylons at the entrance to Cockburn Sound, immediately south of the port of Fremantle, southern Western Australia, on 10 January 1984, Mr Clayton Bryce discovered a medium-sized aeolid nudibranch that he had never seen before (Fig. 1). The specimen was found between middle and low tide levels crawling over mussels

(*Mytilus edulis* L.). It was photographed and taken back to the Western Australian Museum. Unfortunately the animal died before any notes could be made of its appearance in life or habits. Mr Bryce showed me his transparencies in September 1985, and the animal was immediately recognized as new to Australia. Subsequently an anatomical investigation showed it to be *Godiva quadricolor* (Barnard, 1927), an identification that was confirmed beyond all doubt by seeing two slides of South African animals, one of which is reproduced here (Fig. 2). While preparing this report, I received word from Mr Gerhard Saueracker that he had sighted at least a dozen individuals of this species in the Fremantle-Cockburn Sound area between 1980 and 1983. This report describes Mr Bryce's specimen in some detail to enable immediate recognition whenever and wherever further specimens are found.

Besides being a new record for Australia, this particular species is of importance in two other areas of research. The position and scope of the genus *Godiva*, of which *G. quadricolor* is the type species, needs appraisal in a phylogenetic context and the occurrence of *G. quadricolor* in temperate Western Australian waters is vexing zoogeographically. Both these aspects (i.e., phylogenetic systematics and zoogeography), which are addressed in this paper, are currently receiving vigorous attention in zoological circles. This paper is the first of an intended series that I will publish in this Journal discussing phylogenetic systematics and zoogeography of Australian nudibranchs.

## FAMILY FACELINIDAE VAYSSIÈRE, 1888 *Godiva quadricolor* (Barnard, 1927) (Figs 1-13)

### SYNONYMY

*Hervia quadricolor* Barnard, 1927, p. 203, pl. 20, figs 9, 10.

*Godiva quadricolor* (Barnard): Macnae, 1954, pp. 23-25, text figs 14-16; Edmunds, 1964, pp. 26, 27; Lemche, 1964, pp. 56, 57; Baba & Hamatani, 1965, pp. 108, 109; Edmunds, 1977, pp. 302, 303; Rudman, 1980, pp. 160, 171; J. Garcia & F. Garcia, 1984, p. 14.

*Godiva* Macnae has been placed on the Official List of Generic Names in Zoology with the name number 1717 (I.C.Z.N., 1966, Opinion 778). The name *quadricolor* Barnard, as published in the binomen *Hervia quadricolor* (type species of *Godiva* Macnae), has been placed on the Official List of Specific Names in Zoology with name number 2148 (I.C.Z.N., 1966, Opinion 778).

### DESCRIPTION OF AUSTRALIAN SPECIMEN

When crawling in the fully extended state (Fig. 1), the animal (WAM 339-86) was approximately 30 mm long. Its body, which was elongate and widest at the level of the first ceratal cluster, was evenly rounded (circular in cross section) and relatively high. The foot was broader than the back and it tapered posteriorly to a long, narrow tail; anteriorly the foot was extended into two, relatively short tentaculiform processes. The anterior margin of the head was bilobed. The prominent oral tentacles were very elongate (twice the length of the rhinophores), narrow, circular in cross section, and they tapered evenly and gradually to sharply pointed extremities. The rhinophores were tall, circular throughout their length, and they tapered to pointed extremities. The rhinophores appeared smooth to the naked eye and under low magnification, but higher magnification (> 10 times) revealed numerous, tiny, low, flat pustules over the entire surface. One photograph of the living animal gave the impression that its rhinophores possessed about five, indistinct, well separated annulations on their proximal third, but annulations could not be detected on the rhinophores when the animal was preserved so I assume it had contracted its rhinophores immediately before being photographed.

From the photographs, it is obvious that the cerata were assembled in distinct clusters with the widest gap between the first (i.e., pre-pericardial) and second (i.e., post-pericardial) clusters. The ceratal clusters were arranged in symmetrical arches on either side of the midline apart from the posterior pairs which were in short oblique rows. All the anterior clusters possessed multiple rows





Figure 1: *Godiva quadricolor*, crawling length approx. 30 mm; found on mussels between mid- and low tide levels, beacon pylon at entrance to Cockburn Sound, southern Western Australia, 10 January 1984. Photo: C. Bryce.



Figure 2: *Godiva quadricolor*, crawling length approx. 20 mm; collected intertidally at Hottentot's Huisie, Oudekraal, Atlantic coast of Cape Peninsula, Cape Town, South Africa, May 1981. Photo: T.M. Gosliner.

of cerata, but the actual number of cerata within a cluster was impossible to determine as most of the cerata had been autotomized when the animal died. Each cerata was elongate and fusiform, and the largest cerata were situated closest to the dorsal midline. The genital apertures were located on the right side at the base of the anterior limb of the first ceratal cluster. The renal pore was situated immediately in front of the base of the anterior limb of the second ceratal cluster (i.e., it is interhepatic). The anus opened high inside the arch of the second ceratal cluster on the right side (i.e., in the cleioproctic position).

The body wall was translucent, the upper half being suffused with pale fawn and darkening mid-dorsally. Numerous, small, irregular, bluish-white speckles overlaid this ground colour particularly dorsally where, over the pericardium and back, they coalesced into blotches. A narrow, cream streak with a mid-central, brown hair line extended mid-dorsally the full length of the tail. The foot and its tentaculiform processes were translucent white. The head in front of the rhinophores was suffused with orange-brown pigment; that behind the rhinophores was pale, translucent cream. The oral tentacles displayed the most distinctive element of the colour pattern. Their distal third was pale creamish-white dorsally in contrast to the remaining (i.e., proximal) two-thirds over which the brownish orange (most intense dorsally) colour was interrupted dorso-laterally by a sharply defined, pale, watery sky blue streak that extended to the base of each rhinophore, gradually widening as it did so. The rhinophores were translucent; their distal third being uniform, pale, creamish yellow in weak contrast to the proximal two-thirds which was brown. There was a faint brown ring at the very base. All the cerata were similarly coloured; the translucency of their epithelium allowed the narrow, chocolate-brown digestive diverticulum to be discerned with ease. Many cerata possessed a dusting of white pigment over their epithelium. The cnidosac was cream or creamish yellow. Below the cnidosac (i.e., towards the upper fifth of the cerata) was a sky blue ring that was more intensely blue than the colour of the streak on the oral tentacles. Below this blue ring (i.e., towards the upper third of the cerata) was a slightly broader orange ring. The blue ring was not contiguous with either the yellow cnidosac above or the orange ring below.

The uniseriate radula contained 30 teeth of which the youngest one was unthickened. All the teeth consisted of a highly arched basal plate with tapered extensions at the postero-lateral corners. The anterior margin was moderately protracted (i.e., extended well beyond the basal plate) and it culminated in a strong, sharp pointed, smooth bladed cusp. Flanking the cusp were five or six (exceptionally seven or eight), strong, narrow, elongate, primary denticles (Figs 3-5) and one tooth also had considerably weaker secondary denticles arising between the primary ones from the blade (Figs 4, 5). The primary denticles decreased progressively in size with the outermost always being smallest. The actual number of primary denticles was found to vary both between and within teeth i.e., there were different numbers of denticles on either side of the blade. Subdenticles were never present on the sides of the primary or secondary denticles.

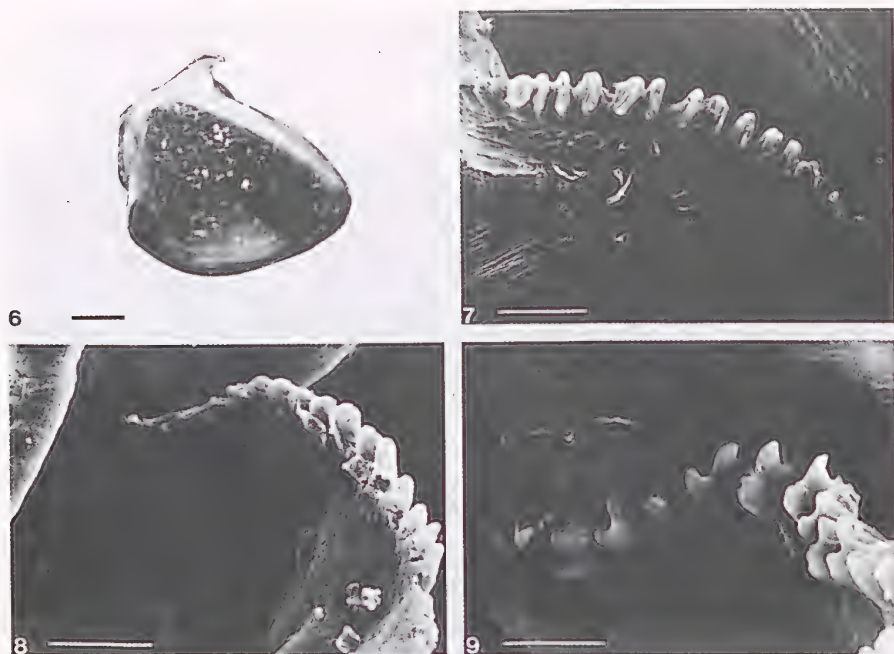
The jaws (Fig. 6) measured 7.1 mm in vertical height and 8.6 mm in maximum length. Their shape was not quite ovate, being slightly elongate antero-posteriorly. Both jaws were symmetrical and, when viewed in profile, both were strongly convex. In outline, the jaw's sides formed an inequilateral triangle. The posterior side was longest (8.9 mm) with a slightly convex curve. The postero-ventral corner was somewhat produced and relatively acute. The ventral side was straight. The upper two-thirds of the anterior side was heavily cuticularized and it bore a flange that extended, as a thin and transparent shield, beyond the jaw's margin. Immediately adjacent to this flange, the apical section of both jaws bore numerous, irregular, short, cuticularized ridges. The lower third of the anterior side had a shallow notch. The tapering masticatory process was relatively short (i.e., approximately one-third the length of the posterior edge) and thin. Its dorsal margin possessed a single row of tall, cuticularized denticles that were fairly even in size. The denticles closest to the jaw's hinge on the attached region of the masticatory border were absent (presumably worn away through use) but it was possible to count 25 on the free region of the masticatory border. Examination with the SEM revealed that the 13 innermost denticles (i.e., those on the proximal region of the free masticatory border) were peg-like with rounded, unnotched apices (Fig. 7), and the 12 outermost (i.e., the remaining denticles nearer the distal extremity of the free masticatory border) denticles were bilobed (Figs 8, 9) and one was serrated (Fig. 9).

The diallic reproductive system was relatively simple (Fig. 10). The ovotestis, which entirely filled the posterior half of the visceral cavity, was composed of about 30, discrete, dorso-ventrally



Figures 3-5: SEM's showing radular structure of Australian *Godiva quadricolor*. 3, dorsal view of radular teeth (numbers 23 [on left hand side]-27 [on right hand side]) towards older end of radula; 4, profile of same teeth (numbers 23-26) to show denticulation; 5, single radular tooth (number 24) enlarged to show secondary denticles between the primary ones. Bars (in Figs 3 and 4) = 0.1 mm and (in Fig. 5) = 0.05 mm.





Figures 6-9: Jaw structure of Australian *Godiva quadricolor*. 6, entire left jaw laid flat showing inner surface, Bar = 2 mm; 7, SEM of simple (i.e., unclenched) denticles on proximal region of free masticatory border; 8, SEM of denticles (simple proximally and bilobed distally) on distal section of free masticatory border; 9, SEM showing detail of bilobed denticles near distal extremity of free masticatory border. Bars (in Figs 7 and 8) = 0.1 mm and (in Fig. 9) = 0.05 mm.

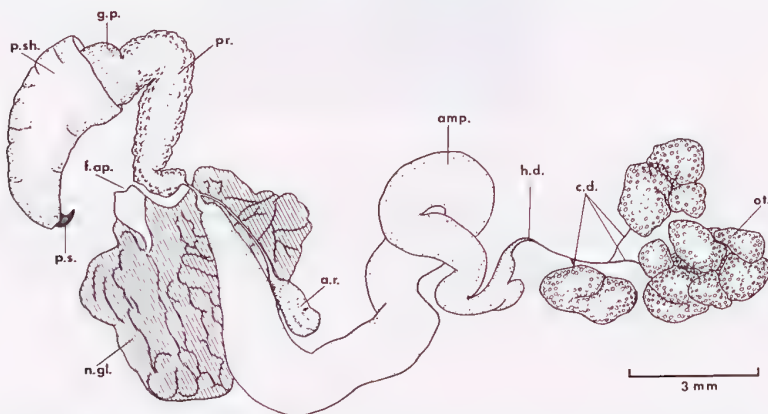
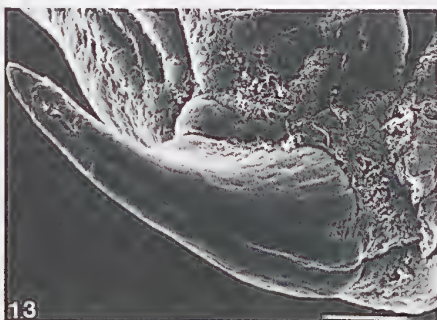


Figure 10: Diagrammatic view of structure of untraveller reproductive organs of Australian *Godiva quadricolor* (penial sheath not removed; only about one quarter of gonadal follicles shown). Abbreviations: amp. = ampullar region of hermaphrodite duct; ar. = allosperm receptacle; c.d. = collecting ducts from ovotestis follicles; f. ap. = female genital aperture; g.p. = glandular proximal region of penis; h.d. = proximal section of hermaphrodite duct; n.gl. = nidamental glands; ot. = ovotestis follicles (detail shown in only one); p.s. = penial spine; p.sh. = penial sheath; pr. = prostatic vas deferens.



Figures 11-13: SEM's of terminal male genitalia of Australian *Godiva quadricolor*. 11, right profile of entire penis with terminal spine (penial sheath not removed), Bar = 0.05 mm; 12, right lateral view showing detail of penial spine; 13, dorsal view showing detail of penial spine and longitudinal groove on outer face. Bars (in Figs 12 and 13) = 0.1 mm.

compressed follicles, each consisting of minute, spherical acini. Approximately 200 acini were present in the anteriormost follicle. The collecting ducts and proximal hermaphrodite duct were exceedingly fine; the latter soon expanded into a long ampulla that continued to enlarge along its length, being the duct of greatest diameter (and hence most easily recognizable) in the entire reproductive system. The ampulla was almost circular in cross section and was completely filled with spermatozoa. The proximal section was arranged into a figure of eight and it was compressed onto the rear of the genital mass. The distal section passed anteriorly without decreasing in diameter. The two halves of the nidamental glands (i.e., the translucent cream mucous gland and milky-white albumen gland) folded so as to sandwich the ampulla laterally. The ampulla eventually constricted to a short distal hermaphrodite duct, gave off a side branch to the single allosperm receptacle, and passed — whilst still very thin — into the vas deferens. The vas deferens was immediately enlarged into a prostate gland and it was glandular for its entire length, being smaller in diameter than the ampulla. The prostate passed into the large, muscular, elongate and slightly curved penis which was surrounded by a muscular sheath (Figs 10, 11). The proximal section of the penis (i.e., that part immediately adjacent to the prostate gland) seemed to possess numerous, distinct, lobular glands but this was not confirmed histologically. A sharp-pointed, curved, cuticular spine (Figs 11-13) measuring 0.4 mm in length projected from the tip of the penis and pointed backwards. The SEM revealed the presence of a narrow, relatively shallow groove along the outer, convex face of the penial spine (Fig. 13). This groove, which was continuous with the terminal opening of the penis, did not extend to the very tip of the spine but ended in a cavity one-tenth of the distance before the end of the spine. The duct to the allosperm receptacle was very long, three times the length of the receptacle, and narrow. The receptacle itself pointed rearwards and was surrounded by the nidamental glands laterally and convolutions of the ampulla posteriorly. In this particular animal, the allosperm receptacle was not expanded, indicating the specimen was virgin. In mated animals the receptacle is much larger, longer, and sausage-shaped.

## ADDITIONAL MATERIAL

Mr Saueracker has provided his additional sightings of *Godiva quadricolor* in southwestern Australia. Apparently none of these specimens was collected:

- 1 specimen (approx. 40 mm crawling length), Outer Estuary, Swan River, southwestern Australia, 1979 or 1980.
- 2 specimens (approx. length of larger specimen 50 mm), North Mole area, Fremantle, southwestern Australia, 1982.
- Approx. 10 specimens, 1-6 metres, Palm Beach, Rockingham, Cockburn Sound, southwestern Australia, 1983.

## REMARKS

The striking external features of *Godiva quadricolor* (Figs 1 and 2) are its translucent body and foot, long tail, long oral tentacles, smooth rhinophores, pale blue streak extending from the rhinophores dorso-laterally down each oral tentacle and elongate cerata with conspicuous blue and orange rings below the yellow cnidosac. Its behaviour is also characteristic — highly active, pugnacious, readily "bristling" the cerata when disturbed and autotomizing the cerata with little provocation.

The body shape, proportions and arrangement of external appendages, colour, shape of radular teeth, and details of jaws of this Australian specimen of *Godiva quadricolor* perfectly match those of southern African animals. (Barnard's (1927) type locality is False Bay, near Cape of Good Hope, South Africa.) The reproductive system, and especially the terminal male genitalia, are also identical. The only differences were the greater number (five or six, exceptionally seven or eight) of primary denticles on all radular teeth and presence of secondary denticles on one tooth in this Australian specimen (Figs 3-5) as compared with only three or four primaries and no secondary denticles in the southern African material.

There is a more recent and more thorough description of South African *Godiva quadricolor* by Macnae (1954). It was based on large numbers of living specimens, so intraspecific variability



was taken into account, and this is apparently considerable as regards colour. Macnae (1954, p. 23) explained how the colours on the cerata varied in their extent; indeed he stated that (presumably any) "one or more of them may be reduced to a vestige or absent altogether". Fortunately the problem of intraspecific colour variation cannot confuse the identification of *G. quadricolor* because all the Australian specimens exactly matched Barnard's (1927) original material in coloration.

Within Australian waters, there are no other known aeolids that could easily be confused with *Godiva quadricolor*, even in the field. Its size, shape, coloration, behaviour and essentially littoral occurrence are reminiscent of the *Austraeolis* species (i.e., *A. ornata* (Angas) and *A. westralis* Burn), but they have shorter oral tentacles, shorter annulate rhinophores, numerous distinct blue spots on the body and foot, and they lack coloured streaks on the oral tentacles and rings on the cerata. In coloration of the cerata only, *Spurilla australis* Rudman is superficially close to *G. quadricolor*; however, despite having two similarly coloured rings on its cerata, *S. australis* has them in reverse order i.e., the orange one is closer to the cnidosac. The only other species of *Godiva* reported from Australia, *G. rachelae* Rudman, is completely different in coloration — it has a pair of orange lines on each side of the head, the lower two-thirds of the cerata is reddish orange, the distal section of the digestive gland is purple and there is a single creamish yellow ring just below the apex of each ceras.

Gosliner (1980) recorded *Godiva quadricolor* from Hawaii and identified Zahl's (1959, p. 523) colour photograph as belonging to that species. However, Dr Gosliner has subsequently studied living specimens of true *G. quadricolor* from South Africa (see Fig. 2) and he now believes the Hawaiian animals represent a distinct species (pers. comm., 1986). Certain disagreements in coloration and reproductive system are also apparent to me between the descriptions of South African and Western Australian material on one hand, and Hawaiian material on the other. Judging from Zahl's photograph and Gosliner's description, Hawaiian animals differ in possessing a white streak along the front edge of the foot and tentaculiform processes and a more or less continuous pale blue line bordering the foot. The tail has a white mid-dorsal streak on its upper surface. The rhinophores are banded in orange-brown and cream. The body is translucent with nebulous pale blue patches. The sky blue dorso-lateral streak is absent from the oral tentacles. The translucent cerata have scattered pigmentation consisting of creamish white pigment, as diffuse yet broad rings, over their outer surface. The chocolate brown digestive diverticulum is straight and narrow, and it tapers gradually to an exceedingly fine distal extremity. The radula of Hawaiian animals appears to be identical to that of South African ones. Gosliner (1980) indicated a spherical allosperm receptacle in Hawaiian animals and he also mentioned a somewhat different orientation for that organ with respect to others of the reproductive system. Closer investigations may reveal even more differences and confirm that the Hawaiian animals represent a new species.

## PHYLOGENETICS

*Hervia quadricolor* Barnard is the type species, by original designation, of the genus *Godiva* Macnae. When Macnae established *Godiva*, he nominated its two principal diagnostic characters (i.e., the most important features by which it could be differentiated from other favorite aeolid genera) as "cerata are inserted in two or more series" [within each cluster] and "rhinophores are either simple or wrinkled". Additional characters shared by *G. quadricolor* and other favorite genera were tentaculiform antero-lateral foot corners, protracted cusp to, and strong primary denticles on, radular teeth and penis "armed with a single terminal hook or unarmed." The fact that the three most important characters of the six (i.e., ceratal arrangement, rhinophoral ornamentation and penial armature) encompassed more than one state meant that interpretation of the generic limits was bound to be controversial and ambiguous, as indeed it has been. What is required now is a critical reappraisal of all the characters of *Godiva quadricolor* to separate the shared "primitive" ones (i.e., plesiomorphs) from the unique "advanced" or derived ones (i.e., apomorphs) and, using only the latter ones, to redefine the genus. This discrimination between characters and stress on apomorphies forms the basis of Hennigian phylogenetic systematics. The utility of this redefined genus will be in reappraising its several presently contained species and in testing its relationships, in a phylogenetic context, with other favorite genera.

Table 1 lists the relative plesiomorphy or apomorphy, as related to all aeolids (i.e., not just members of the family containing *Godiva*), of 13 morphological characters. Polarities for constructing this table were determined by examining the character state distribution across many aeolid genera (especially those taxa generally accepted as "primitive") and by reference to outgroups such as the Arminoidea and Dendronotoidea. The majority (11) of these 13 characters exist in the apomorphic state in *Godiva* making it a relatively advanced aeolid genus. The situation remains unaltered when *Godiva* is assessed in a similar way against other genera in its family (Table 2). In this analysis, nine of the 11 characters exist in the apomorphic state. Of these nine apomorphies, however, only one is unique to *Godiva* (i.e., autapomorphic) — the curved, cuticularized, terminal penial spine. It is this character alone that must form the basis, in an exclusive sense, for the definition of the genus.

Therefore I advocate a redefinition of *Godiva* with the following exclusive set of character states: Medium-sized facelinid aeolids with smooth rhinophores; antero-lateral foot corners tentaculiform; oral tentacles moderately long; majority of cerata grouped (in two to eight rows) within arches; genital opening in front of first cluster; anus cleioproctic; uniseriate radula with protracted cusp and primary (and occasionally secondary) lateral denticles; single row of denticles on jaw's masticatory border; reproductive system with elongate ampulla, short and thick prostatic vas deferens, very elongate stalk to allosperm receptacle; penis with a curved, cuticularized, terminal spine.

This combination of characters, which is sufficient to warrant continued recognition of *Godiva* as a genus, gives *Godiva* a much narrower scope than that envisaged by Macnae (1954). By doing this, the uncertainty created by Macnae (1954) and perpetuated by Edmunds (1964), Rudman (1980) and J.C. Garcia & F.J. Garcia (1984) can be dispelled. Baba & Hamatani (1965, p. 108) have already pre-empted my action. Besides *G. quadricolor* only two other species, *G. rachelae* Rudman and Gosliner's "*G. quadricolor*" from Hawaii, now fall within the ambit of *Godiva*. Incidentally, *G. rachelae* also possesses cuticularized ridges on the apex of the jaws like those in *G. quadricolor*. Further evaluation of this new character and the longitudinal groove on the penial spine within facelinids may demonstrate them to be additional autapomorphies of *Godiva*. Indeed, an investigation of aeolids for other characters of taxonomic utility is overdue.

Eight other aeolids that have been included in *Godiva* at one time or another should now be excluded. Each is discussed separately.

*Rizzolia australis* Bergh, 1884. Macnae (1954) included this insufficiently described eastern Australian aeolid in *Godiva* when he initially diagnosed the genus. However Burn (1966, p. 31) has subsequently synonymized it with *Austraeolis ornata* (Angas), an act I wholeheartedly support. Gosliner (1980, p. 57) apparently missed this synonymy when he commented on the similarity between *R. australis* and members of the genus *Setoeolis* Baba & Hamatani. Incidentally, the genus *Rizzolia* Trinchese has now been rejected as a junior objective synonym of *Cratena* Bergh (I.C.Z.N., 1966, Opinion 776).

*Hervia ceylonica* Farran, 1905. This, plus the following three species were all placed in *Godiva* by Macnae (1954). This particular taxon is problematic because of the inadequacy of the original description. I agree with Rudman (1980, p. 164) that the species is unrecognizable.

*Cuthona* (*Hervia*) *emurai* Baba, 1937. This species has a smooth penis with a large, soft flap proximally. On penial structure alone, Baba & Hamatani (1965) proposed the new monospecific genus *Shinaneolis* to accommodate *emurai*.

*Rizzolia modesta* Bergh, 1880. Baba (1937) transferred this Japanese species to *Hervia* and, realizing the taxon then became a secondary homonym of *Hervia modesta* Bergh, 1871, amended the specific name to *japonica*. This replacement has now been sanctioned by the International Commission on Zoological Nomenclature (I.C.Z.N., 1966, Opinion 778). Macnae (1954) indicated this species belonged to *Godiva* but, because it lacks a penial spine, it should be more appropriately located in *Dondice* (as suggested by Er. Marcus, 1958, p. 66) or *Sakuraeolis* (as suggested by Baba & Hamatani, 1965).

*Hervia rosea* Bergh, 1888. This species, which has apparently not been recognized since its original

TABLE 1. Relative Plesiomorphy and Apomorphy of Aeolid Characters.

Plesiomorphic	Apomorphic
Distinct notal brim	No notal brim
Antero-lateral corners of foot rounded	Antero-lateral corners produced into tentaculiform extensions
Lamellate (or annulate) rhinophores	Rhinophores smooth or papillate, or with other ornamentation
Ceratal arrangement irregular	Cerata arranged in oblique rows or arches
Many cerata per cluster	Few cerata per cluster
Genital opening behind first ceratal cluster	Genital opening in front of first ceratal cluster
Renal pore interhepatic	Renal pore behind first post-pericardial cluster
Anus below notal brim, i.e., below ramifications of the digestive gland (pleuroproctic)	Anus more dorsal, and within interhepatic space (acleioproctic) or within (or just behind) pre-pericardial cluster (cleioproctic)
Oral glands composite	Oral glands simple
Multiseriate radula (i.e., rachidian plus lateral teeth present)	Uniseriate radula (i.e., only rachidian present)
Cusp on rachidian protracted (i.e., tooth cuspidate)	Cusp on rachidian withdrawn (i.e., tooth pectinate)
Masticatory border of jaw smooth	Masticatory border with several rows, or only a single row, of denticles
Penis simple	Penis elaborated with (soft or hard) external ornamentation and/or internal glands

TABLE 2. Relative Plesiomorphy and Apomorphy of Facelinid Characters.

Plesiomorphic	Apomorphic
Antero-lateral corners of foot produced into tentaculiform processes	Antero-lateral corners rounded
Lamellate (or annulate) rhinophores	Rhinophores smooth
Extensive branching of digestive gland in body	Reduction in branching of digestive gland in body
Many cerata per cluster	Few cerata per cluster
Cerata clustered in oblique rows	Cerata clustered in arches
One or 2 rows of cerata in each arch	More than 2 rows of cerata in each arch
Genital opening behind first ceratal cluster (i.e., interhepatic)	Genital opening in front of first ceratal cluster
Anus cleioproctic	Anus behind second ceratal cluster
Blades of rachidian with primary denticles only	Blades of rachidian with secondary denticles between primary ones or subdenticles on cusp
Masticatory border of jaw with several rows of denticles	Masticatory border with only a single row of denticles
Penis simple	Penis elaborated with (soft or hard) external ornamentation and/or internal glands



description, lacks a penial spine. Therefore it should be transferred to *Dondice* or *Sakuraeolis*, if indeed it is a member of the Facelinidae.

*Favorinus horridus* Macnae, 1954. This species is obviously not congeneric with *Eolis alba* Alder & Hancock, the type species of *Favorinus* M. E. Gray. Risso-Dominguez (1964) erected the genus *Phyllodesmiopsis* for it. Edmunds (1964) transferred it to *Godiva* on plesiomorphies of the penial and prostate glands. Rudman (1981) transferred it to *Phyllodesmium* because, amongst other characters, it had synapomorphies of flattened cerata, lack of cnidosacs and radular teeth morphology.

*Dondice banyulensis* Portmann & Sandmeier, 1960. On the basis of its anatomy, J.C. Garcia & F.J. Garcia (1984) transferred this Mediterranean species to *Godiva*. Actually it has markedly different rhinophores, radular teeth and penis to *G. quadricolor*, so it cannot be located in *Godiva*.

*Godiva rubrolineata* Edmunds, 1964. The shared similarities with *G. quadricolor* are plesiomorphs and the genital aperture opens further rearwards (i.e., below the rear limb of the pre-pericardial ceratal cluster). Neither *Sakuraeolis* nor *Shinaneolis* can accommodate this species since both are characterized by penial elaborations. Perhaps *Dondice* or *Setoeolis*, in which the penis is simple, would be more appropriate genera for this tropical western Atlantic species. Gosliner (1980, p. 57) favoured the latter genus for its placement.

## DISCUSSION OF THE FAMILY NAME

In a substantial and provocative review, Miller (1974) proposed the merging of 10 nominal aeolid families (Facelinidae, Favorinidae, Babakinidae, Pteraeolidiidae, Cratenidae, Caloriidae, Phidianidae, Myrrhinidae, Herveliidae and Glaucidae) into one because of similarities in structure of the jaws, radular teeth, glands of the alimentary system, penial glands and armature, and branching of the ducts of the reproductive system. The two autapomorphies advanced by Miller to support unification of these taxa to this single enlarged family related to possession of simple oral glands and subjective behavioural traits. I must record here that the second characteristic is not exhibited by all the species I have studied; for example, *Pteraeolidia ianthina* is neither "nervous", "fast moving", "aggressive", "voracious" nor "cannibalistic" when alive. Incidentally, the enlarged family had to take the name Glaucidae which, as Miller himself remarked, was unfortunate because *Glaucus* and *Glaucilla* are the most aberrant forms. This taxonomic necessity may have prevented some workers from embracing the entire concept (e.g., Thompson & Brown, 1984, p. 104).

In overview, it seems to me that a critical review was necessary. The earlier splitting of these aeolids between several families (most workers recognized only three or four) was excessive and it exaggerated minor differences instead of stressing fundamental similarities. This scheme therefore, completely obscured the great natural coherence of all the aeolid taxa concerned. This amalgamation has now gained general acceptance amongst opisthobranch systematists (Gosliner, 1980; Rudman, 1980, 1981; Edmunds & Just, 1983; Thompson & Brown, 1984). Edmunds & Just (1983, p. 193) have provided a diagnosis for the family. On reviewing the genera myself (from both living material and literature), I find only *Glaucus* and *Glaucilla* really do stand apart. Synapomorphies are: foot narrower than body; anterior foot corners rounded; very short oral tentacles; rhinophores on the sides of the head; cerata flattened laterally; cerata arranged on (up to 4) lateral swellings; heavily cuticularized oral tube; reduced primary denticles; pleustonic life style; inverted dorso-ventral posture. In my opinion, such a suite of autapomorphies justifies the placement of these two genera in a separate family, Glaucidae. Analogous classification schemes already exist in the Prosobranchia and Bivalvia where the Struthiolariidae and Tridacnidae, whilst obviously derived from the Strombidae and Cardiidae respectively, are given separate familial status in recognition of their radiation into new ecological zones and consequent acquisition of gross morphological novelties. That leaves the remaining nine aeolid units which, in accord with Miller (1974) I regard as monophyletic, condensed into a single family. This enlarged family must take the name Facelinidae. Whether or not the genus *Facelina* Alder & Hancock, upon which it is founded, is a synonym of *Phidiana* Gray (a most contentious and unsettled point amongst present day opisthobranch systematists) has no bearing on the eligibility of the taxon Facelinidae Vayssi re, 1888 to stand as the family name. This ruling follows the (arguably unfortunate) Copenhagen

decision of the International Commission on Zoological Nomenclature that the choice of a family name should be decided by priority even when the generic name on which it is based has been abandoned as a junior synonym. That ruling is now embodied in the Principle of Priority incorporated into the present International Code (I.C.Z.N., 1985, Articles 23 (a) and (d)). Precedents of the application of this ruling already exist in molluscan taxonomy; for example, the family name *Psammobiidae* Fleming, 1828 takes priority over *Garidae* Stoliczka, 1870, even though the genus *Psammobia* Lamarck, 1818 is a subgenus or junior synonym of *Gari* Schumacher, 1817 (I.C.Z.N. 1970, Opinion 910). *Phidianidae* Odhner in Franc in Grassé, 1968 is therefore a synonym of *Facelinidae*.

Gosliner (1980, p. 39) and Edmunds & Just (1983, pp. 193, 200) have reached the same conclusion as I do regarding the *Facelinidae* and *Glaucidae*, although they still exclude the monotypic genus *Pteraeolidia* from the *Facelinidae*. I also support Gosliner's (1980) additional contention that the subfamilies *Facelininae*, *Favorininae*, *Crateninae* and *Hervellinae* are unnecessary since their contained species level taxa are probably polyphyletic.

## ZOOGEOGRAPHY

The occurrence of a population of *Godiva quadricolor* in temperate waters of southwestern Australia has thrown up another piece in a vexing zoogeographical jigsaw puzzle. This identification of *G. quadricolor*, whilst certainly providing a new record for Australia, behoves biogeographers and malacologists to account for the species' arrival because it can be explained under more than one zoogeographical hypothesis.

*Godiva quadricolor* was first described from False Bay, South Africa (Barnard, 1927). Its distribution from False Bay near the Cape of Good Hope to Port Alfred and relative abundance throughout that range, as noted by Macnae (1954), led to the assumption that it was endemic to the temperate waters of southern Africa (Edmunds, 1977). The first hypothesis for its occurrence in Western Australia does not invoke any natural mechanism, but is by way of shipping across the Indian Ocean. Either adults could have been transported on the outsides of ships' hulls [believed to have been the means responsible for the present day virtually cosmopolitan distribution of at least one other nudibranch, *Thecaera pennigera* (Willan, 1976; Willan and Coleman, 1984)] or larvae could have been transported within the ballast tanks of seagoing vessels (Carlton, 1985; Williams & Griffiths, 1986). Entrained ballast water is a much underestimated present day mode of transoceanic dispersal of marine organisms. This shipping hypothesis would appear to have more evidence to support it than any alternative hypothesis. By this, I refer firstly to the recent colonization of several other foreign marine organisms in the same area of southwestern Australia, essentially that centered on the port of Fremantle. Documented cases amongst the Mollusca are those of the bivalves *Theora lubrica* (Chalmer et al., 1976) and *Musculista senhousia* (Slack-Smith & Brearley, 1987). Second is the apparent confinement, at present, of *G. quadricolor* to the Fremantle-Cockburn Sound area. Third is the fact that Western Australia receives approximately half the total Australian national commercial shipping each year (Williams et al., 1982). Finally is the undisputed introduction by shipping of another endemic temperate southern African nudibranch, *Polycera capensis*, to Sydney Harbour in the 1920's (Burn, 1978). Edmunds (1977) put forward a protocol in order to recognize marine animals that might have crossed, or be capable of crossing, oceans on boat hulls. At all stages of the organism's life cycle it should be possible to show that: (1) suitable foods do grow on boat hulls; (2) some individuals are occasionally found on boats; (3) the species is restricted on one side of the ocean to the vicinity of ports (at least to begin with); (4) the species is morphologically identical on both sides of the ocean. With the knowledge that Edmunds (1977) did actually find one specimen of *G. quadricolor* on a boat hull in Ghana, the last three criteria are all satisfied unequivocally in the case of *G. quadricolor*.

It is possible that some of the other endemic South African molluscs that have turned up in southwestern Australia such as *Haliotis spadica* (Macpherson, 1953 as *Haliotis sanguinea*), *Nassarius kraussianus*, *Bullia annulata* and *Cabestana cutacea dolaria* (Wells & Kilburn, 1986) might also have been introduced by shipping. Yet none of these species has established a breeding population, as judged by persistence of records through time. Alternatively some as yet unexplained natural

zoogeographic mechanism could have allowed them, and *Godiva quadricolor* too, to cross the Indian Ocean from west to east.

Gosliner's (1980) report of *Godiva quadricolor* from Hawaii, if correct, would have allowed another zoogeographical hypothesis account for the presence of *G. quadricolor* in southwestern Australia; that of possession of a continuous Indo-Pacific distribution. However, I feel significant objections have eliminated this hypothesis. First is Dr Gosliner's own present belief (pers. comm., 1986, 1987) that Hawaiian and South African specimens are not conspecific. Since his examination of Hawaiian animals, Dr Gosliner has studied South African ones at first hand and he now recognizes significant morphological differences do exist (see Remarks section). Second is Edmunds' (1977) query that, if *G. quadricolor* were to have a continuous Indo-Pacific distribution, it should have been found at other intervening localities in the Pacific Ocean where nudibranch faunas have been relatively well investigated such as Japan, the Marianas Islands, the Marshall Islands, New Caledonia, eastern Australia and New Zealand. This is particularly true since *G. quadricolor* is essentially an intertidal species, and also it is relatively large and distinctively [Edmunds (1977, p. 303) said "gaudily"] coloured.

In closing, I suggest time itself will be the best test between the competing hypotheses of man-aided transportation or natural transoceanic dispersal. If the Western Australian population persists and expands its range and/or if *Godiva quadricolor* occurs in other temperate ports in the world, the former hypothesis will be vindicated.

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# Reproductive periodicity of the Chiton *Acanthopleura hirtosa* on intertidal platforms in the Perth area of Western Australia

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## ABSTRACT

The reproductive periodicity of populations of *Acanthopleura hirtosa* on three intertidal platforms in the Perth metropolitan area was studied using both gonad indices and histological analysis of gonad tissue. Both methods showed that the animals spawned in a single discrete period from April to June. The largest influx of juveniles into the population occurred from June to August, but recruitment was at a low level, suggesting that the animals survive for at least two years. Reproductive periodicity of *A. hirtosa* is compared with that known for other chitons.

## INTRODUCTION

During the summer of 1981/82 a research program was begun into the molluscs of intertidal beachrock platforms in the Perth metropolitan area. The initial objective was to quantify the hypothesis that a significantly greater component of the mollusc assemblages on platforms at the western end of Rottnest Island was of tropical species than occurred on the inshore platforms of the metropolitan coastline (Wells, 1985). With the closure of the platforms to fishing of abalone and other gastropods in the summer of 1982, the research was expanded into a three year study to examine molluscan assemblages on the platforms to provide basic information for fisheries scientists to use in formulating management policies for the platforms. One early suggestion was that seasonal closures could be used to protect platform species during the reproductive season. However, most of the research on reproductive periodicity of platform species, including molluscs, has been done at Rottnest I. (see Black and Johnson, 1983) and little is known of reproductive seasonality on inshore platforms. Only three species had been studied: *Brachidontes ustulatus*



(Lamarck, 1819) (Wilson and Hodgkin, 1967); *Turbo torquatus* Gmelin, 1790 (Joll, 1980); and *Nodilittorina unifasciata* (Gray, 1825) (Wells, 1984). To develop further information on reproductive periodicity of molluscs four additional species were examined. The four species were studied in separate years, partially by students from the Western Australian Institute of Technology, and used differing techniques. Because of this data for the four species are being presented in a series of separate papers: *Haliotis roei* Gray, 1827 (Wells and Keesing, in prep.); *Cantharidus pulcherrimus* (Wood, 1828) (Wells and Keesing, 1987); and *Patelloida nigrosulcata* (Reeve, 1825) (Wells and Keesing, in press). The present paper reports on the reproductive periodicity of the chiton *Acanthopleura hirtosa* (Blainville, 1825).

Nine species of chitons were found on the platforms during the study. Most were small forms present in low density and biomass, but two large species, *A. hirtosa* and *Onithochiton quercinus* (Gould, 1846), were important components of the fauna of the bare zone at the seaward edge of the platforms. The relative importance of *A. hirtosa* and *O. quercinus* varied considerably on the different platforms: *O. quercinus* was dominant at Garden Island and *A. hirtosa* at both Trigg Island, Cottesloe, and Waterman. Because two of these platforms (Trigg I. and Cottesloe) are heavily affected by human activity, *A. hirtosa* was selected for study.

In addition to its importance in the bare zone *A. hirtosa* is also common at the base of the limestone cliffs at the landward margin of the platforms. *A. hirtosa* is endemic to Western Australia, with a range of from Esperance to Shark Bay. Aside from remarks on its taxonomy, the only published information on *A. hirtosa* is a paper on its temperature tolerance by Kenny (1958). For many years *A. hirtosa* was placed in the monospecific genus *Clavazona*, but it was recently transferred to *Acanthopleura* (Ferreira, 1986).

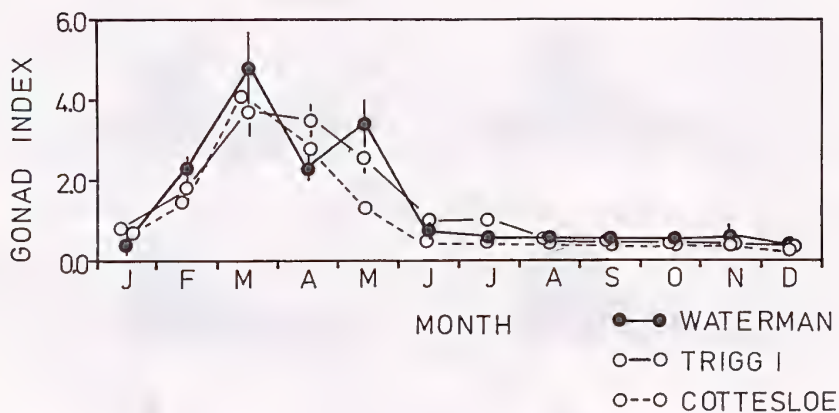
## MATERIALS AND METHODS

Size frequency data on *A. hirtosa* were collected monthly from January to December 1985 at the base of the cliffs at Waterman, Trigg I. and Cottesloe. Because these chitons adhere tightly to the rock surface it was not possible to measure their length *in situ* with accuracy. Instead maximum width of the widest shell plate was measured with calipers to the nearest 1 mm. All data presented relate to shell width. A sample of 39 individuals over the full size range of the species was collected at Trigg I. on 28 June 1985. The animals were relaxed and both plate width and total length measured. The data were fitted to a line of best fit and produced the equation  $Y = 1.47 + 2.02 X$  where  $X$  is width in mm and  $Y$  is length in mm. The equation was statistically significant and had an  $r$  value of 0.97.

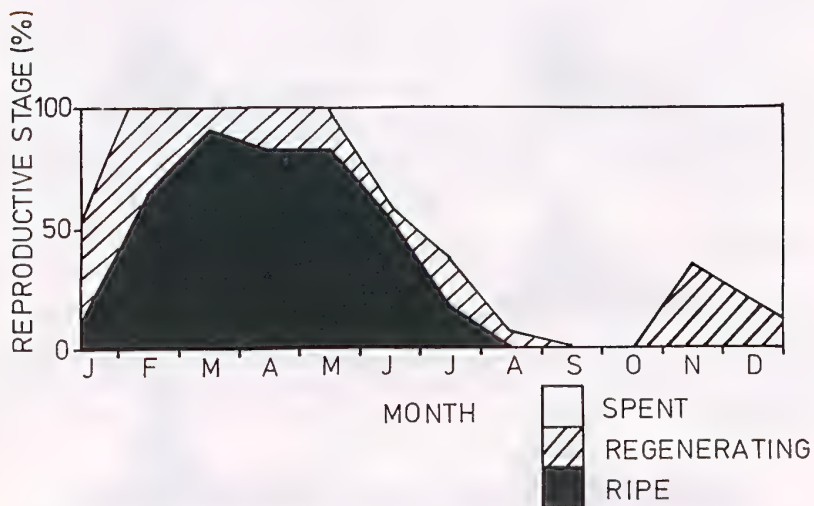
To examine reproductive periodicity 10 *A. hirtosa* were collected monthly from each platform, in areas not used for the size frequency measurements. Larger chitons at least 15 mm in plate width were used. The animals were preserved in 10% formalin and total wet weight later measured on a Sartorius electronic balance. The gonads were then dissected out and weighed separately. The gonad index was calculated as the ratio of gonad weight divided by total weight multiplied by 100. To examine histological state the gonads were then fixed in Bouin's solution for 12 hours, dehydrated through an alcohol series, cleared in xylene, embedded in paraffin wax and sectioned at 7  $\mu$ m. The sections were stained with haematoxylin and eosin. The slides were examined microscopically and assigned to reproductive states of ripe, spent, and regenerating. As sample sizes were small and no differences between platforms were observed data on gonad state from the three platforms were pooled.

## RESULTS

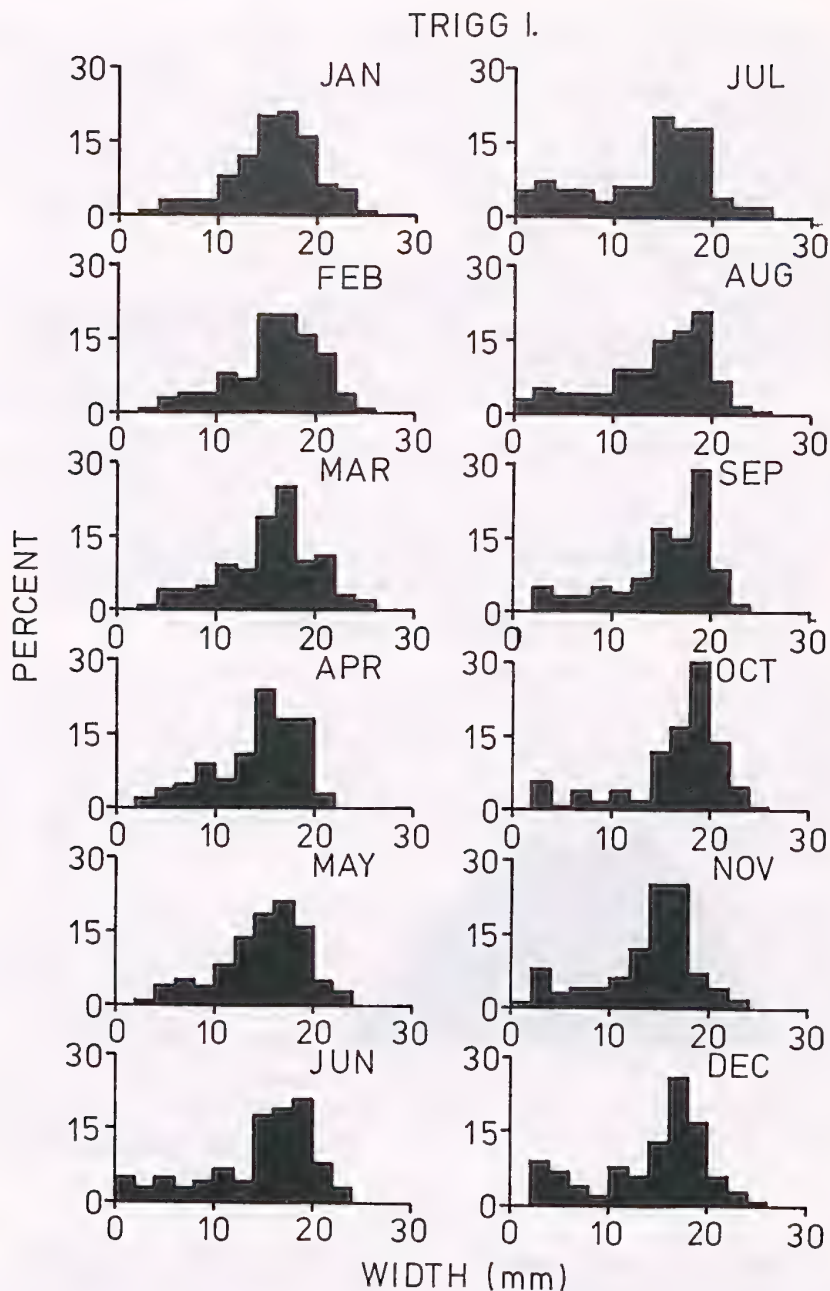
The gonad index was below 1.0 for *A. hirtosa* on all three platforms at the beginning of sampling in January 1985 (Figure 1). The index increased to about 2.0 by February and 4.0 in March. The index then declined steadily from April to June, when it reached 0.7, indicating that spawning had taken place during this period. For the remainder of the year the gonad index remained low, in the region of 0.5. The pattern was similar for all three platforms, with Waterman having the highest gonad index of 4.8 in March, followed by a decline to 2.3 in April and a recovery to 3.4



Gonad index of *Acanthopleura hirtosa* collected at monthly intervals on three intertidal platforms in the Perth metropolitan area from January to December 1985. Means  $\pm$  1 S.E. are shown. Where no S.E. is shown the error was smaller than the circle showing the mean.



Reproductive states of *Acanthopleura hirtosa* collected at monthly intervals on intertidal platforms in the Perth metropolitan area. Data from Waterman, Trigg I. and Cottesloe have been pooled.



Size frequency characteristics of *Acanthopleura hirtosa* at Trigg I. at monthly intervals from January to December 1985.



in May. Despite the greater variability at Waterman the general pattern matches that found at Trigg I. and Cottesloe.

Data for reproductive state (Figure 2) closely parallel the gonad index. At the beginning of sampling in January 1985 four animals were ripe, 13 were spent and 13 regenerating. By February 19 were ripe and in March 27 of 30 were ripe. The number of ripe animals remained high until May, when 25 were ripe and then declined steadily until August, when there were no ripe individuals. No ripe animals were found after July. All animals in September and October were spent; some regenerating individuals were found in November and December. These data suggest that *A. hirtosa* spawned from May to July, while the gonad index suggests spawning occurred from April to June.

The size frequency data show that except for small numbers of juveniles in the second half of the year the populations of *A. hirtosa* on the three platforms were unimodal, with modes occurring in the 15-20 mm plate width range. The maximum recorded width was 28 mm, which indicates a length of 58 mm. Histograms for the Cottesloe and Waterman platforms show that the populations were composed of mature individuals throughout the year and there was no period of major recruitment into the population during the year. The largest influx of small individuals occurred at Trigg I. in the period of June-August (Figure 3).

## DISCUSSION

Pearse (1979) has recently summarized the available studies on reproductive periodicity in chitons. Most species have a single discrete reproductive season which may be short or last for several months. Superimposed on the annual cycle may be short term fluctuations in spawning intensity on a monthly or semimonthly basis. Populations of a single species in different geographic areas may have different breeding cycles (Glynn, 1970; Pearse, 1979). Sufficient data are available for only two areas for reproductive periodicity of a group of species to be compared: in the temperate waters off the west coast of North America most chiton species studied spawn in the coldest part of the year (late winter and spring) (Pearse, 1979), while in the tropical waters off Puerto Rico the period of greatest spawning activity was the warmest season (autumn) (Glynn, 1970).

*A. hirtosa* off Perth spawns in a discrete period of three months during the autumn, when water temperatures are still warm. No attempt was made to search for short term variations in spawning intensity, nor for variations in populations from different geographical areas. The species occurs over a wide geographical range, from Esperance on the south coast to Shark Bay on the west coast, in which there are substantially different temperature regimes, and different reproductive seasonality in various areas would not be unexpected.

A number of chitons have been reported to brood embryos, including several species in southern Australia (Turner, 1978); no such brooding behaviour was found in *A. hirtosa*.

Few data are available on the life expectancy of chitons, but those which have been studied live for only a few years (Pearse, 1979). Very few young individuals entered the population of *A. hirtosa* on Perth platforms in 1985, precluding an estimate of growth rate and time required to reach maturity. The size frequency graphs for all months showed that the population was comprised primarily of large individuals. This shows that *A. hirtosa* lives for at least two, and probably more, years.

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